

Oak, chestnut and fire: climatic and cultural controls of long-term forest dynamics in New England, USA

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Abstract

Aim Despite decades of study we have limited insights into the nature of the pre-European landscape of the north-eastern USA and the forces and changes that shaped modern forest patterns. Information on such long-term forest dynamics would provide critical insights into the relationships among environmental change, land-use history and biotic responses and is greatly needed for conservation planning. To address these issues we used modern, historical, and palaeoecological approaches to reconstruct the 3500-year history of a New England upland region dominated by oak and (formerly) chestnut forests and to interpret the interactions among climate change, natural and human disturbance, and site factors in controlling vegetation patterns and dynamics at different spatial scales.

Location The study focused on a broad upland ridge dominated by oak forests in the north-central Massachusetts town of New Salem. Detailed palaeoecological analyses were undertaken of wetland (Chamberlain Swamp) and lake (Lily Pond) basins in order to reconstruct local to regional scale vegetation dynamics, which were interpreted within the context of regional vegetation data from central Massachusetts.

Methods Palaeoecological methods were used to reconstruct the vegetation, fire and land-use history of the local and subregional vegetation from the two basins and to place these in the context of regional information on vegetation and climate change based on other published data. Historical information including maps, archaeological and census data, and vegetation information were gathered for the landscape and areas surrounding the coring sites. Vegetation sampling in transects adjacent to the swamp coring area included tree cores for dendrochronological reconstructions.

Results Stand, landscape and regional forest dynamics were most strongly driven by climate, notably an apparent cooling and increase in moisture availability *c.* 1500 yr BP, and European land-use activities commencing 260 yr BP. However, the abundance of oak and chestnut (fire-tolerant, sprouting species) and the distribution of hemlock (fire-intolerant) at a stand to landscape scale were also influenced by fire, which, in turn, varied with climate and human activity. Despite, or perhaps as a consequence of ongoing disturbance by fire and presumably windstorms in this hurricane-prone region, the pre-European period was marked by two 1000+ year periods of remarkably stable forest composition, separated by an abrupt compositional shift. In contrast, over the past 260 years the vegetation has changed rather continuously in response to human activity, producing stand, landscape and regional patterns that are novel as well as recent in origin.

The results indicate that chestnut was a major component of some pre-European landscapes in New England, in part because of occasional fire, and that cultural and physical factors have interacted over millennia to control vegetation patterns and dynamics. Our analyses also suggest that the composition of low diversity forests can be

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remarkably stable over millennia. The range of ecological, cultural and management insights afforded by this study underscores the fundamental utility of very long-term research in science and policy development.

Keywords

Human disturbance, natural disturbance, climate change, fire, oak, chestnut, hemlock, palaeoecology, dendrochronology, land use, New England.

INTRODUCTION

Ecologists have increasingly recognized that ecosystem structure, composition and function are strongly conditioned by history and that, as a consequence, landscape interpretations and conservation strategies must be based on an understanding of processes and events oftentimes occurring in the distant past (Clark, 1989; Sprugel, 1991; Birks, 1996; Foster, 1999, 2000; Franklin *et al.*, 2000; Motzkin & Foster, 2002). This awareness of history has been motivated by several common observations: all ecosystems are dynamic as a consequence of disturbance and environmental change; many biological processes, including ecosystem development, unfold over century-long periods; and these dynamics generate imprints or legacies in soils or ecosystem structure and composition that may endure for decades or centuries (Davis & Botkin, 1985; Abrams, 1996; Foster *et al.*, 1998a, b; Harding *et al.*, 1998; Compton *et al.*, 1999; Donohue *et al.*, 2000; McLachlan *et al.*, 2000; Foster *et al.*, 2002a). The clear linkage between ecosystem history and current pattern and process makes it imperative that long-term perspectives are integrated into ecological and applied studies (Cissel *et al.*, 1998; Foster & Motzkin, 1998; Swetnam *et al.*, 1999; Foster, 2000, 2002; Knops & Tilman, 2000).

In New England, where the landscape has been transformed by human activity during at least the past 400 years, historical studies provide many insights into modern forest conditions (Whitney, 1994; Foster & O'Keefe, 2000; Hall *et al.*, 2002; Eberhardt *et al.*, 2003). A history of colonial deforestation and intensive agriculture followed by farm abandonment, natural reforestation and forest growth has produced a largely forested landscape that is strongly shaped by its past (Cronon, 1983; Motzkin *et al.*, 1996; Foster, 1999). At a subregional scale (e.g. across central Massachusetts), broad similarities in historical land use have homogenized the resulting forests and reduced the compositional variation that was controlled by regional climate gradients at the time of European settlement (Foster *et al.*, 1998a; Fuller *et al.*, 1998; Parshall *et al.*, 2003). At the stand scale novel vegetation dynamics and species assemblages were initiated by human activity even in the least disturbed parts of the landscape, the permanent woodlots that were cut in the eighteenth and early nineteenth centuries but never cleared like the surrounding agricultural areas (Foster *et al.*, 1992; McLachlan *et al.*, 2000). Across the landscape today forest composition, structure and ecosystem process are strongly conditioned by the prior pattern of forest cutting,

pasture or plowing (Wofsy *et al.*, 1993; Motzkin *et al.*, 1996, 1998, 1999, 2002a,b; Aber & Driscoll, 1997).

Previous long-term studies of forest communities and landscape patterns in New England have been restricted to lowland forests dominated by hemlock or spruce, largely because these sites often contain small hollows, wetlands, or deep organic soils that provide good palaeoecological records of stand-level changes (cf. Bradshaw & Miller, 1988; Foster *et al.*, 1992; Foster & Zebryk, 1993; McLachlan *et al.*, 2000; Schauffler & Jacobson, 2002). Consequently, there is almost no stand or landscape-scale information on the pre-settlement vegetation, disturbance regimes or forest dynamics of the extensive upland areas that are dominated by oak, chestnut (formerly), red maple, black birch and other hardwood species. Insights into the dynamics of these areas are critical as they dominate the New England forest landscape and include the areas most strongly affected by natural and human disturbance processes, including fire, windstorms, and pre-historical and colonial land-use practices (cf. Boose *et al.*, 2001; Parshall & Foster, 2002). Currently, upland forest areas are the intense focus of broad-scale conservation planning and support the most valuable and actively harvested timber stands (Golodetz & Foster, 1996; Barbour *et al.*, 1998; TTOR, 1999; Foster, 2000; BioMap, 2001; Berlik *et al.*, 2002). Long-term studies of these uplands would enable more prudent conservation strategies by broadening our understanding of forest response to intense human activity. In particular, such studies would strengthen the assessment of the apparent regional decline of oak, an important wildlife and timber genus (Lorimer, 1989; Abrams, 1992, 1996). In the ongoing discussion concerning the history of oak and factors responsible for its changing abundance across the eastern USA there has been little information pertaining to the New England region (Abrams, 1996; Orwig *et al.*, 2001).

In the current study, we apply palaeoecological, historical and ecological approaches across a broad upland area in central Massachusetts to investigate the long-term (3500-years) dynamics of oak-dominated forests and landscape patterns in the context of regional vegetation change. To develop a lengthy, but local, forest history we obtained sediment cores from the margins of a small wetland basin (40 × 70 m) on a wide upland ridge that is dominated by oak (Fig. 1). The basin is currently surrounded by extensive oak forest on three sides, but has a discrete stand of hemlock along the eastern margin. Pollen assemblages from the margins of such small basins include strong representation of forest composition within *c.* 50 m (cf. Jackson

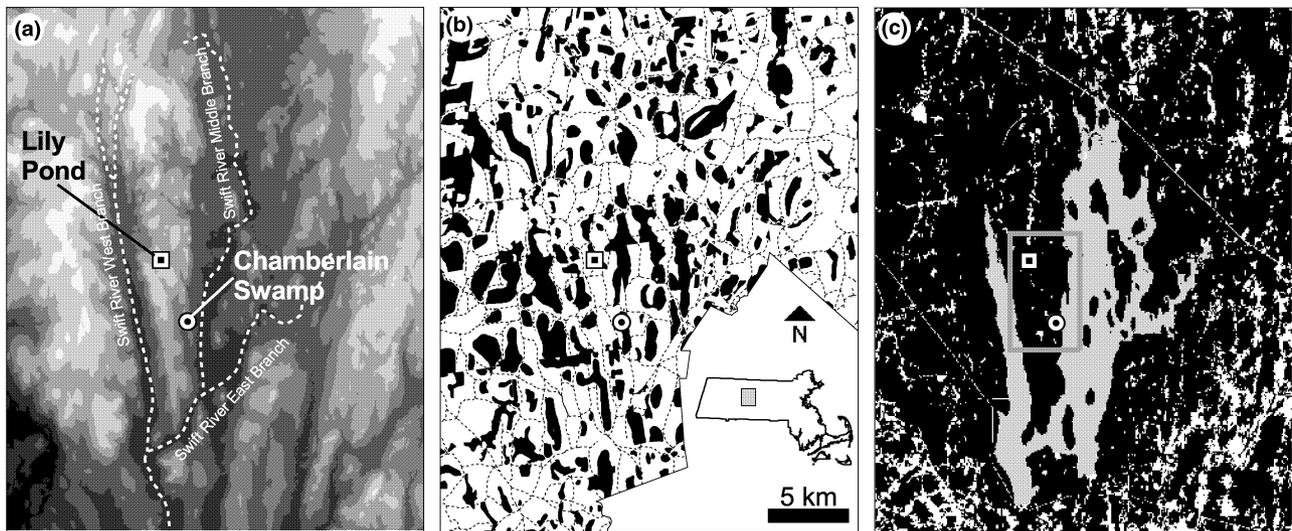


Figure 1 The study area in north-central Massachusetts (see inset map in 1b) depicting: (a) topography (50-m resolution from 50 to 450 m a.s.l.), the Swift River (white broken lines) before flooding of the Swift River Valley to construct the Quabbin Reservoir in 1938, and the location of Lily Pond (square) and Chamberlain Swamp (circle); (b) forest cover (black), open land (white) and road network (black broken lines) in 1830 at the approximate height of deforestation and agricultural activity. Note that historical data for the south-eastern portion of the area are not available; and (c) forest cover (black), open land (white) and the Quabbin Reservoir (grey) in 1985. Forest cover in the study area (*c.* 69,000 ha) has increased from 27 to 89% from 1830 to 1985 (Foster *et al.*, 1998b). Outlined rectangle in (c) depicts the region illustrated in Fig. 2.

& Wong, 1994; Sugita, 1994; Calcote, 1998; Parshall, 2002); and by obtaining cores adjacent to the oak and hemlock sides of the basin we sought to contrast the long-term histories of these forests. To provide additional detail on the two stands we undertook vegetation and dendro-ecological studies in both forests and gathered historical information on land use and land cover for the landscape, township and region. The long-term histories of the two stands were placed in a landscape context by analysing the sediments from a small pond (Lily Pond, New Salem) located 5 km to the north on this broad ridge. Because of the larger surface and pollen collecting area of the 3-ha pond, its pollen record should provide a strong signal of the vegetation within 5–10 km (Jacobson & Bradshaw, 1981; Jackson, 1990; Sugita, 1993). The regional context for the interpretation of stand and landscape dynamics is provided by a network of palaeoecological sites and historical data across southern New England (cf. Foster *et al.*, 1998b; Fuller *et al.*, 1998; Cogbill *et al.*, 2002; Hall *et al.*, 2002; Appendix 1).

By examining the long-term development of upland oak forests from a stand, landscape and regional perspective the study addresses specific questions:

1. What is the pre-settlement (pre-European) history of natural and human disturbance, environmental change, and vegetation dynamics of the oak-dominated forest and the mosaic of oak and hemlock stands?
2. How did these processes and patterns change with European land-use activity and lead to the development of the modern forests and landscape pattern?

3. Do upland forests exhibit an analogous range of dynamics and yield similar ecological insights as the lowland hemlock forests?

Study area

The study focused on the Central Uplands physiographic region of Massachusetts, which is characterized by north-south trending ridges, hills and valleys ranging from 150 to 350 m a.s.l. (Fig. 1). The shallow soils are brown podzols of the Shapleigh Series, composed of rocky fine sandy loam that developed in a thin mantle of sandy glacial till derived from underlying Palaeozoic granites, gneisses and schists (Mott & Fuller, 1967). The vegetation is representative of the Transition Hardwoods – White Pine – Hemlock forest region, and the climate is moist, cold temperate (Westveld & Committee on Silviculture, New England Section, Society of American Foresters, 1956). The oak forests investigated are typical of extensive oak areas that dominate much of the upland region.

In the early twentieth century the landscape setting was comprised of a long broad ridge (*c.* 5 × 15 km) with the town of Prescott in the north centre, bordered to the east by the wide Swift River Valley and to the west by a narrow valley and tributary stream (Figs 1 and 2). In 1938, the ridge was isolated into what is called the Prescott Peninsula when the Swift River was dammed to the south to flood both valleys. Prescott and three other towns (Greenwich, Enfield, Dana) in the valley and adjacent uplands were discontinued, all residents were relocated, and access to the Prescott

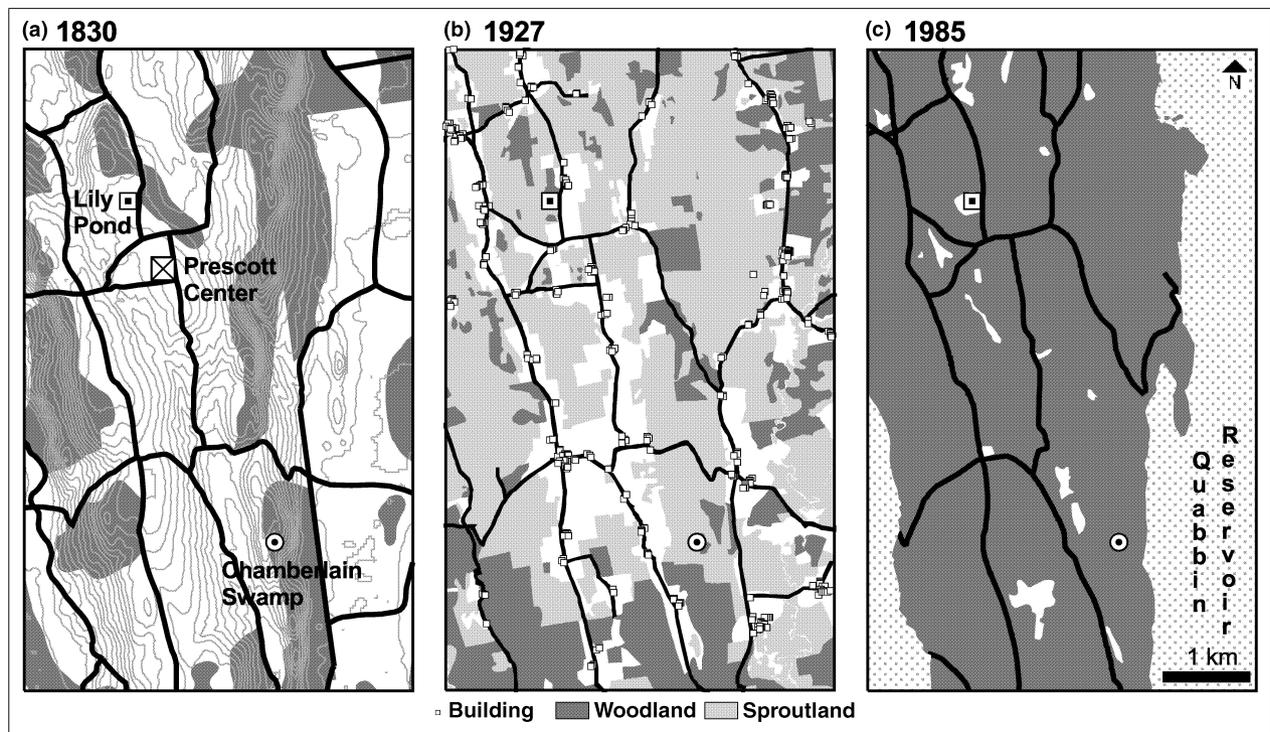


Figure 2 Detailed map of the study area depicting the distribution of forest (shaded) and open land (white) in (a) 1830, (b) 1927 and (c) 1985. In (a) topography is depicted in 10-m contours, ranging from 140 to 340 m a.s.l.; (b) buildings are shown as squares and forest land is separated into sproutland (light shading) of young, recently cut forest and woodland (dark shading) of older forest; (c) water (light shading) of the Quabbin Reservoir surrounds the Prescott Peninsula.

Peninsula was restricted. The resulting 10,000-ha Quabbin Reservoir serves as the primary source for metropolitan Boston's water (Conuel, 1981; Barten *et al.*, 1998). Chamberlain Swamp (the small wetland basin) occupies an oak-dominated ridge (Kelley's Hill) on the east side of the Prescott Peninsula (Figs 1 and 2). Red oak (*Quercus rubra*) dominates the forest with scattered black and white oak (*Q. velutina* and *Q. alba*), red maple (*Acer rubrum*), black birch (*Betula lenta*), yellow birch (*B. alleghaniensis*), pignut hickory (*Carya glabra*), white pine (*Pinus strobus*), white ash (*Fraxinus americana*), and in the swamp, black gum (*Nyssa sylvatica*). Occasional chestnut (*Castanea dentata*) sprouts occur in the understory along with ericaceous shrubs, principally huckleberry (*Gaylussacia baccata*) and blueberry (*Vaccinium* spp.). A hemlock (*Tsuga canadensis*) stand extends 30-m upslope from the eastern swamp margin to the edge of the ridge, which then descends abruptly downslope 150 m in elevation to the Quabbin Reservoir and the bottom of the Swift River Valley (Figs 1 and 2). Hemlock is restricted to this small stand and is absent from the broad ridge around Chamberlain Swamp. Downed chestnut wood, stumps and poles dating to mortality from the chestnut blight around 1910 (Kittredge, 1913; Paillet, 2002) are found across the ridge.

Lily Pond is located 5 km northwest of Chamberlain Swamp, just north of the former centre of the town of Prescott (Figs 1 and 2). The watershed is dominated by

forests of red oak with lesser amounts of paper birch (*B. papyrifera*), black birch, red maple and white pine. The 3-ha pond occupies gentle relief, has seasonal inflowing and outflowing streams, and a discontinuous wetland fringe.

History of the Swift River landscape

Although pre-historic information for north-central Massachusetts is highly incomplete, there is ample evidence of active use of the Swift River valley and adjoining upland areas by Indian populations during the Late Woodland period (1000–400 yr BP) preceding European settlement (Dincauze, 1980; Massachusetts Historical Commission and M. Mulholland, unpublished data, T. Malstedt, pers. comm.). A recent archaeological survey indicates many habitations including seasonal (spring–summer, fall–winter) and hunting camps on the uplands and more substantial sites near the valley bottoms. Diverse and important resources in this region include the mosaic of woodlands, wetlands, meadows, streams and ponds; a great abundance of mast-bearing trees (oak, chestnut, hickory and beech); access to anadromous fish populations in the Swift River; a regionally important source of soapstone for manufacture of stone implements; and the low-lying, protected and relatively warm valley (D. Dincauze, M. Mulholland and T. Malstedt, pers. comm.). Maize agriculture arrived in southern New England c. 1000 yr BP, but there

is scant evidence for its horticulture in central Massachusetts or much of southern New England (Parmenter, 1898; Bendremer, 1993; Bragdon, 1996; Chilton, 1999; cf. Motzkin & Foster, 2002). There are ethnohistoric accounts from the Swift River area of Indian burning of forests to promote secondary growth and increase deer browse (D. Dincauze, pers. comm.); similar descriptions from coastal Massachusetts have been cited as evidence for widespread manipulation of upland vegetation with fire (Day, 1953; Wood, 1977; Cronon, 1983; Morton, 1967; but see Motzkin & Foster, 2002). Palaeoecological studies indicate an increasing importance of pre-European fire from the cooler Uplands to the warmer and lower Connecticut Valley and Eastern Lowlands (cf. Patterson & Backman, 1988; Fuller *et al.*, 1998; Parshall & Foster, 2002). This gradient of fire may reinforce the regional pattern of climatic control over vegetation, favouring northern hardwoods and hemlock in the Uplands and oak and hickory in the Lowlands and Valley (Fuller *et al.*, 1998).

European settlement in the Swift River area began in 1730 and over the next century the valley and gentler uplands were cleared for pasture, meadows, upland hay fields and cropland (Parmenter, 1898). By the early nineteenth century the four towns supported 3000 people and many local industries based on wood and agricultural products. Detailed land cover maps from 1830, the approximate peak of deforestation and agriculture, indicate that more than 70% of the forest was cleared for pasture and tillage, including much of the area around Lily Pond (Fig. 1; cf. Foster *et al.*, 1998b). In contrast, Chamberlain Swamp was part of a large woodland that extended along the eastern part of the ridge and down adjoining valley slopes (Fig. 2). This and other permanently wooded areas were cut repeatedly to provide fuel and other resources for rural populations and industries (Garrison, 1991; Foster *et al.*, 1998b; Foster, 1999). In particular, chestnut wood was highly valued for timber, fencing and railroad sleepers, and the nuts were harvested extensively by people and wildlife (Foster, 1999). White pine, oak and pitch pine timber were also heavily used.

Agricultural abandonment commenced across New England in the mid-nineteenth century although broad valleys with productive soils like the Swift River Valley were maintained in agriculture (Foster & O'Keefe, 2000). Consequently, when the Quabbin Reservoir was created in the 1930s the landscape was a mosaic of open farmland, meadows, swamps, villages and scattered woodlots in the valley and sproutlands (frequently or recently cut hardwoods), woodlands of older trees, second-growth white pine stands on abandoned fields, and small fields on the upland ridges (Fig. 2). Quabbin Reservoir land managers converted open fields to conifer plantations and they continue to manage much of the 30,000-ha reservation for timber products (Barten *et al.*, 1998). Although the forests on the ridge surrounding Chamberlain Swamp had not been logged in the 75 years preceding the study, in 1999 the mature oak was cut intensively (B. Spencer, pers. comm.).

Detailed land-use maps from 1927 show Chamberlain Swamp surrounded by a large sprout woodland with open

agricultural land to the east and west (Fig. 2). Historical sources and field reconnaissance confirm that the woodland area and steep valley slopes were continuously in forest cover and were never cleared. In 1927, the watershed of Lily Pond had sproutland (second-growth cut-over forest) to the north and west, and open land to the east (Fig. 2).

METHODS

Palaeoecology

At Lily Pond, 8.5 m of lake sediment were recovered in 1993 from the pond centre in 3 m of water using a modified Livingstone piston sampler (Livingstone, 1955; Wright, 1967). At Chamberlain Swamp two cores were taken 35-m apart using a 5-cm diameter Russian corer; one core from the west margin adjacent to the oak stand and the second from the east margin and hemlock forest. A duplicate core was taken on the hemlock side with a 10-cm diameter piston corer to provide adequate material for analyses and radiocarbon dating. Cores were transported to the lab, stored at 4 °C and subsampled at 1-cm intervals for pollen, charcoal and loss-on-ignition (LOI). Pollen samples were processed using standard methods, adding a known concentration of *Eucalyptus* pollen suspension to determine pollen and stomate concentrations (Faegri *et al.*, 1989). A minimum of 400 arboreal pollen grains was counted per sample and pollen percentages are based on all terrestrial pollen and spores. Charcoal was counted at 400× magnification using the point count technique on the same slides used to count pollen (Clark, 1982). Stomates were identified and counted simultaneously with pollen on all samples from Chamberlain Swamp (Hansen, 1995; Clayden *et al.*, 1996).

To determine organic matter content by LOI, contiguous 1-cm samples were dried at 95 °C for 6 h and placed in a muffle furnace at 550 °C for 1 h. Ten AMS ¹⁴C dates were obtained from the upper 3.0 m of sediment from Lily Pond; five each at the Woods Hole National Ocean Sciences AMS Facility and University of Arizona, AMS Laboratory. The Russian cores from Chamberlain Swamp were stratigraphically matched with the larger diameter core based on LOI, distinct horizons and other visible changes in colour and texture. One bulk ¹⁴C date from the 10-cm core on the hemlock side of the swamp was obtained at Beta Analytic and was used to date the corresponding levels on the two swamp cores. All dates were converted to calendar years using the program CALIB (Stuiver & Reimer, 1993a,b). The settlement horizon in the pollen diagrams was identified by the rise in agricultural pollen indicators (*Ambrosia*, *Rumex*, Poaceae) and was assigned a date of 1740 (260 yr BP) based on local settlement history (Parmenter, 1898).

To place the data from Chamberlain Swamp and Lily Pond in a broader geographical perspective we compared the Lily Pond record and thirteen other pollen stratigraphies from across central Massachusetts and Connecticut using multivariate analyses (cf. Fuller *et al.*, 1998). These lake

basins had been selected using the same criteria: small (< 10 ha) basins with low to minimal inflow or outflow and with little modern human disturbance in the watershed.

Numerical analysis

Pollen diagrams were zoned using constrained incremental sum of squares (CONISS) cluster analysis with the programme TILIA (version 1.12) developed by Eric Grimm (Illinois State Museum, Springfield, IL, USA). All terrestrial taxa > 2% of the pollen sum were included and data were square-root transformed prior to analysis. Pollen percentage data from all samples from both the oak and hemlock sides of Chamberlain Swamp were combined and analysed in a principal components analysis (PCA) using Psimpoll (version 2.31; Bennett, 1996). Data were selected and transformed using criteria similar to those used for cluster analysis.

For the regional analysis we combined the arboreal pollen data for the last 2000 years from Lily Pond and the thirteen additional sites (see Appendix 1) in a detrended correspondence analysis (DCA), using all taxa reaching an abundance greater than 2%. Similar analyses were conducted on all pre-European and historical (after 260 yr BP) samples. The relationship between pollen (and inferred vegetation) variation and climate was assessed through regression of the centroids of the pre-European and historical sample distributions for each site on axis 1 against the calculated average of growing degree-days for areas within 5, 10 and 20 km of each lake (cf. Fuller *et al.*, 1998; Hall *et al.*, 2002).

Historical tree records

We compiled data on the abundance of major tree taxa at the time of European settlement for all townships in Massachusetts to provide an independent assessment of the historical forest composition (cf. Foster *et al.*, 1998b). The data are witness or boundary trees noted in the original surveys of lots or roads (Cogbill *et al.*, 2002). Each tree notation was recorded, nomenclature was standardized (cf. Cogbill, 2000), and then abundance maps were compiled showing species percentages in each township. Prior analyses of these and comparable proprietor data indicate that they are geographically consistent, show strong relationships with

regional environmental gradients, and demonstrate no apparent bias (cf. Whitney, 1994; Abrams & Ruffner, 1995; Foster *et al.*, 1998b; Cogbill *et al.*, 2002; Hall *et al.*, 2002).

Vegetation survey and dendroecological methods

The age, structure and composition of the overstory vegetation were sampled on the hemlock (east) and oak (west) side of Chamberlain Swamp in three 60-m transects spaced 30 m apart and orientated perpendicular to the swamp margin. Each transect included three 10 × 20 m plots, for a total of nine plots per side (total sample area for each side = 1800 m²). Within each plot, species name and diameter at breast height (d.b.h.) were recorded for every stem > 1.4 m tall and > 2 cm d.b.h. Nomenclature follows Gleason & Cronquist (1991). In each plot, two to three dominant or codominant trees were arbitrarily selected and cored with an increment borer at 1.4 m height for age determination. Cores were air-dried, mounted, sanded and aged under a dissecting microscope. All downed trees, stumps or standing dead trees > 2 cm diameter and originating in each plot were identified by species and size class to estimate the structure, composition and abundance of coarse woody debris and to infer prior stand composition.

RESULTS

Current vegetation and age structure

On the eastern side of the swamp large hemlocks comprised more than 70% of the stems and basal area, red oak represented *c.* 10% of density and basal area and six other species were less abundant (Table 1). On the oak (west) side red oak dominated (56% of basal area) along with eleven additional species (Table 2). Total density and basal area were less than half of that on the hemlock side. Red maple was abundant near the swamp, black birch was evenly distributed across the western slope, and red oak was dominant immediately away from the swamp.

On both sides of the swamp even-aged cohorts of red oak, other hardwoods, or (on the east side) hemlock are *c.* 110 years old (Fig. 3). Recruitment of overstory red oak and hemlock continued from *c.* 1890 to around 1925 on the

Species	Density (ha ⁻¹)	Relative density (%)	Basal area (m ² ha ⁻¹)	Relative basal area (%)
<i>Acer rubrum</i>	33	2.0	1.0	2.0
<i>Betula lenta</i>	61	3.6	1.3	2.6
<i>B. papyrifera</i>	11	0.7	0.4	0.8
<i>Nyssa sylvatica</i>	6	0.3	0.04	0.1
<i>Pinus strobus</i>	17	1.0	1.8	3.4
<i>Quercus rubra</i>	217	12.7	9.5	18.4
<i>Q. alba</i>	11	0.7	0.4	0.8
<i>Tsuga canadensis</i>	1351	79.0	37.1	71.9
Totals	1707	100	51.54	100

Table 1 Abundance of tree species (> 2.0 cm d.b.h.) on the hemlock side of Chamberlain Swamp

Table 2 Abundance of tree species (>2.0 cm d.b.h.) on the oak side of Chamberlain Swamp

Species	Density (ha ⁻¹)	Relative density (%)	Basal area (m ² ha ⁻¹)	Relative basal area (%)
<i>Acer rubrum</i>	239	32.5	2.6	11.0
<i>Betula lenta</i>	139	18.9	3.1	13.1
<i>B. alleghaniensis</i>	33	4.5	1.7	7.4
<i>Carya glabra</i>	67	9.1	0.4	1.6
<i>Castanea dentata</i>	6	0.8	0.01	0.1
<i>Fraxinus americana</i>	17	2.3	0.4	1.8
<i>Hamamelis virginiana</i>	50	6.8	0.5	0.2
<i>Nyssa sylvatica</i>	6	0.8	0.2	0.7
<i>Pinus strobus</i>	11	1.5	0.8	3.4
<i>Quercus alba</i>	6	0.8	0.4	1.7
<i>Q. rubra</i>	156	21.2	13.1	56.0
<i>Q. velutina</i>	6	0.8	0.7	3.0
Totals	736	100	23.9	100

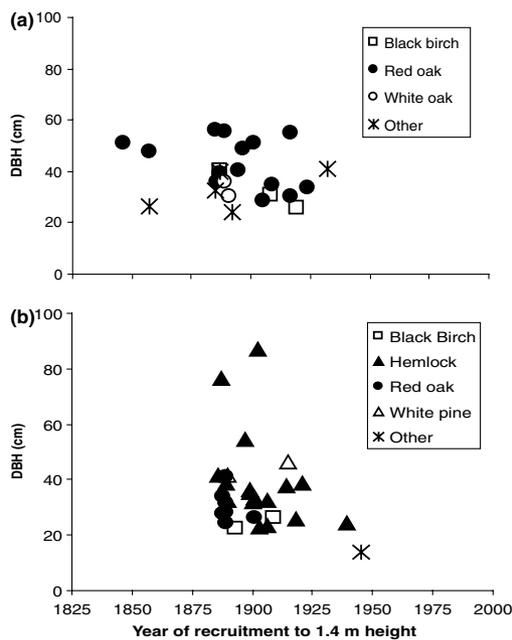


Figure 3 Age and size structure of the forests on the (a) west (oak forest), and (b) east (hemlock forest) sides of Chamberlain Swamp. Trees were cored at 1.4 m height where d.b.h. measurements were taken. The two stands show a similar history, with the majority of trees establishing after 1890. The two older red oaks and one white ash on the oak side exhibit a release (sharp increase) in growth in 1888 suggesting a response to the removal of the surrounding trees by logging. Other species cored include red maple and paper birch.

oak and hemlock sides, respectively, and sapling-sized oaks are found. Two older red oaks on the oak side exhibit an abrupt increase in growth in 1888, suggesting the removal of adjacent trees and establishment of the younger cohort. The large number of cut stumps, standing stems and downed wood of chestnut throughout the area indicate that chestnut was formerly abundant on both slopes (Fig. 4). Chestnut stump densities in the plots ranged from 174 to 274 ha⁻¹ and stump diameters were 4–100 cm (Fig. 4).

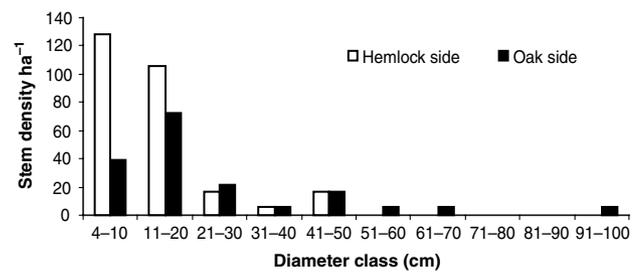


Figure 4 The size distribution of chestnut coarse woody debris located in the vegetation transects on the hemlock (light shading) and oak (dark shading) sides of Chamberlain Swamp. Diameters were measured at the base of stumps or downed wood. Although small diameter material prevails, a few stumps exceeding 50-cm d.b.h. were sampled in the plots and many large stumps are scattered across the slopes and ridge beyond.

Sediment chronology and characteristics

The ten AMS ¹⁴C dates from Lily Pond (Table 3) were calibrated to calendar years (yr BP) and fitted in Tilia using a two-order polynomial to develop the age scale in the pollen diagram (Fig. 5). The three cores from Chamberlain Swamp were matched by similarities in the pollen and sediment stratigraphies, especially LOI and the transition from fibrous to fine-grained sediment, which was dated at 2300 yr BP (Table 3). All cores from Chamberlain Swamp have high organic content (*c.* 80%) in the upper 65 cm (Figs 6 and 7), dropping to *c.* 50% at 72 cm, the transition from fibrous material to finer organic and mineral-rich sediment. Organic content declines to < 20% below 80 cm where sand increases. Through the period of European history the sediments show no change in physical characteristics.

Lily Pond sediments have an organic content of *c.* 40% from 300 to 200 cm. Above 200 cm LOI fluctuates until 120 cm where it reaches a fairly steady 60%. The fluctuations are concurrent with major changes in the pollen record including the expansion of chestnut and an increase in charcoal abundance (Fig. 5). During the historical period

Table 3 Radiocarbon dates and calendar ages for samples from Lily Pond and Chamberlain Swamp

Accession	No. sample ID	Depth (cm) (corrected)	¹⁴ C age (BP)	Error	Calibrated ¹⁴ C (BP)	2σ error
AA-35302	Lily 49–50	49	635	40	582	666–544
OS-18138	Lily 59–60	59	695	50	658	694–555
OS-18139	Lily 81–82	81	740	40	581	667–546
AA-35303	Lily 100.5–101.5	100.5	415	40	500	525–325
OS-18140	Lily 103–104	103	810	45	719	791–665
OS-18141	Lily 125–126	125	1550	50	1414	1541–1314
OS-18142	Lily 147–148	147	1490	40	1352	1512–1301
AA-35304	Lily 151–152	201	1560	45	1417	1541–1333
AA-35305	Lily 200–201	250	2625	55	2750	2846–2555
AA-3467	Lily 244–245	294	3245	50	3467	3628–3361
Beta-97768*	Chamberlain Swamp 42–47	72	2290	70	2336	2350–2120

*Bulk ¹⁴C date from a core used for radiocarbon dating only. All other dates are ¹⁴C AMS.

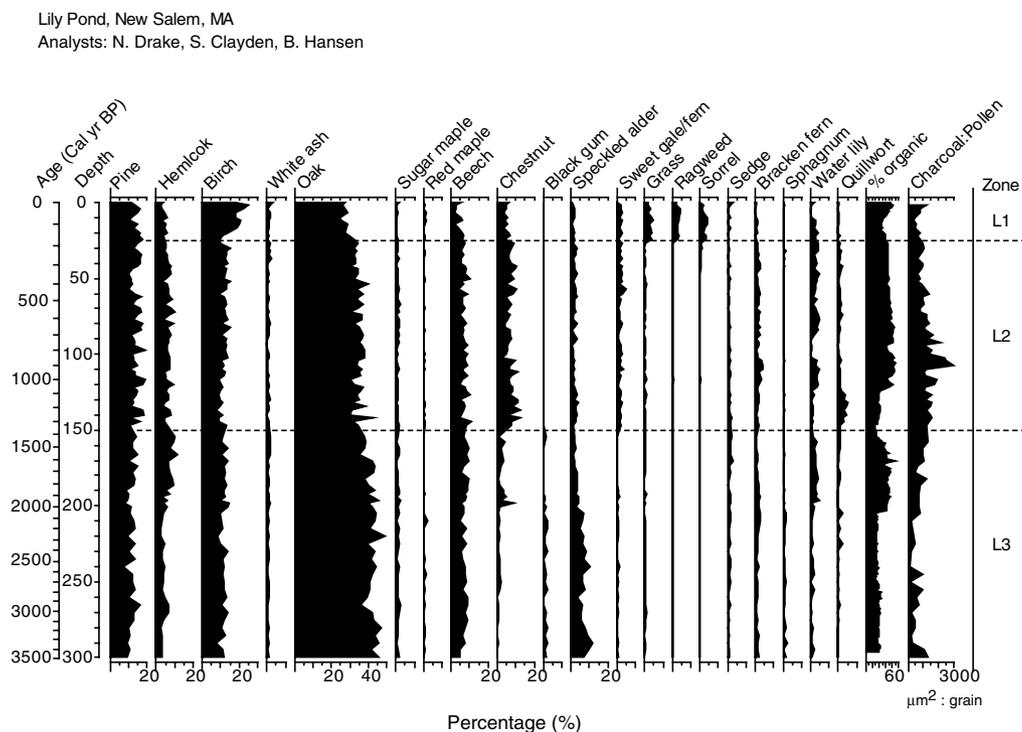


Figure 5 Stratigraphic diagram for Lily Pond illustrating changes in pollen and spore percentages, charcoal and loss-on-ignition with sediment depth and age (cf. Table 3). Stratigraphic pollen zones were identified objectively using the CONISS clustering routine and correspond to the major increase in chestnut and charcoal and decline in oak *c.* 1400 yr BP (L-3 / L-2) and the changes in land cover and pollen associated with European settlement and land use in the mid-eighteenth century (L-2 / L-1). The age-depth model was based on a total of ten AMS radiocarbon dates (Table 3).

LOI parallels the inferred history of land clearance as it declines to 40% at the height of agricultural activity (*c.* 1850 AD) and returns to higher values towards the surface. These changes are presumably driven by erosion and

delivery of mineral material to the lake basin as the forested watershed was cleared for agriculture followed by a decline in mineral inputs as farmland was abandoned and reforested (Francis & Foster, 2001).

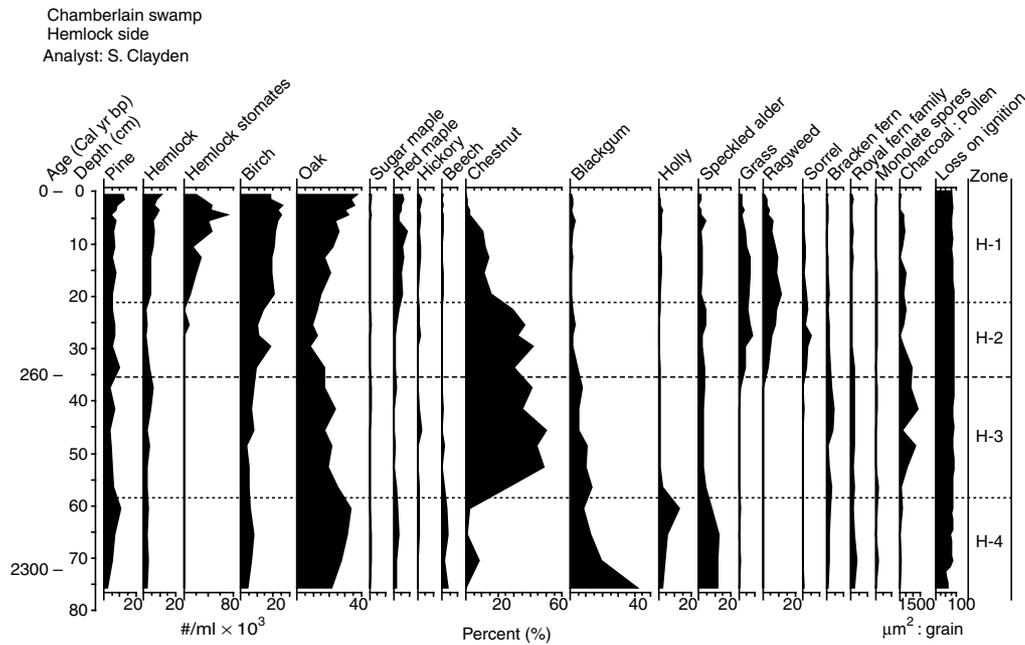


Figure 6 Stratigraphic diagram for the hemlock (east) side of Chamberlain Swamp depicting changes in pollen and spore percentages, hemlock stomates, charcoal and loss-on-ignition, with sediment depth and age based on European settlement (*c.* 1740) and a C-14 date from a correlated core (see Methods). Pollen zones are identified objectively using CONISS. Zone boundaries correspond to the dramatic increase in chestnut and decline in oak and some wetland taxa above 60 cm (H-3 / H-4), European settlement at 35 cm (H-2 / H-3), and the decline in chestnut just below 20 cm (H-1 / H-2). Hemlock stomates occur continuously and in increasing numbers in the upper 25 cm, where they parallel the increasing values of hemlock pollen.

Pollen and inferred vegetation history

Pollen stratigraphy – Lily Pond

Three pollen zones were identified in the Lily Pond diagram based on cluster analysis of pollen percentages (Fig. 5). Throughout, oak is the dominant pollen type (> 25%).

L-3 (3500–1400 yr BP). Oak pollen exceeds 40% with a maximum abundance of 49%. Abundant tree taxa include pine, birch, beech and hemlock. Wetland taxa, including alder (*Alnus rugosa*), black gum and *Sphagnum* reach maximum abundance, and sugar maple, hickory, sedge and bracken fern are present. Chestnut increases from < 1% at the bottom of the zone to > 1% and is consistently present above 200 cm (*c.* 2750 yr BP). Charcoal values are consistently higher than at most sites in the New England Uplands (Backman, 1984; Patterson & Backman, 1988; Fuller *et al.*, 1998).

L-2 (1400–260 yr BP). The abrupt expansion of chestnut, starting at 195 cm and peaking at 13%, distinguishes this zone. Taxa that increase coincidentally with chestnut include hemlock and sweet-gale/sweet-fern (*Myrica-Comptonia*), whereas oak declines to *c.* 30% and the wetland taxa alder, blackgum and *Sphagnum* decline. Quillwort (*Isoetes*), water lily (*Nymphaea*), and bracken fern fluctuate at higher pollen abundance. Charcoal values dip, rise to values approximately double of those in L-3, peak around 900 yr BP, and then decline towards the top of the zone. Organic content is low initially and then rises to high values.

L-1 (260–0 yr BP). The settlement zone is marked by the sharp rise in agricultural and weedy taxa including ragweed (*Ambrosia*), grasses (Poaceae), and sorrel (*Rumex*). Chestnut, oak, beech and hemlock decline, while birch initially declines and then increases to 26% at the top. Quillwort, water lily and bracken decline, particularly at the top. Charcoal values decline slightly and then rise.

Pollen stratigraphy – Chamberlain Swamp

Pollen diagrams from the hemlock and oak side are similar and are divided into four pollen zones described together (Figs 6 and 7). Differences between the diagrams are interpreted as reflecting variation in upland vegetation on the two sides of the swamp.

O-4 and H-4. At the base of both cores upland pollen spectra are dominated by oak with pine and birch. Wetland taxa, including black gum, black alder (*Ilex*) and alder reach maximum abundance and are greatest on the hemlock side. Other taxa at low pollen abundance include beech, red maple, hickory and hemlock (all < 5%). Chestnut percentages are low and fluctuating. Charcoal values are quite low on the hemlock (eastern) side and high on the oak (western) side.

O-3 and H-3. The dramatic expansion of chestnut, which increases to > 40% in both diagrams, defines the beginning of this zone. Chestnut values remain high but decrease slightly through the zone. Chestnut expansion coincides with a decline in oak (to less than half its previous abundance on

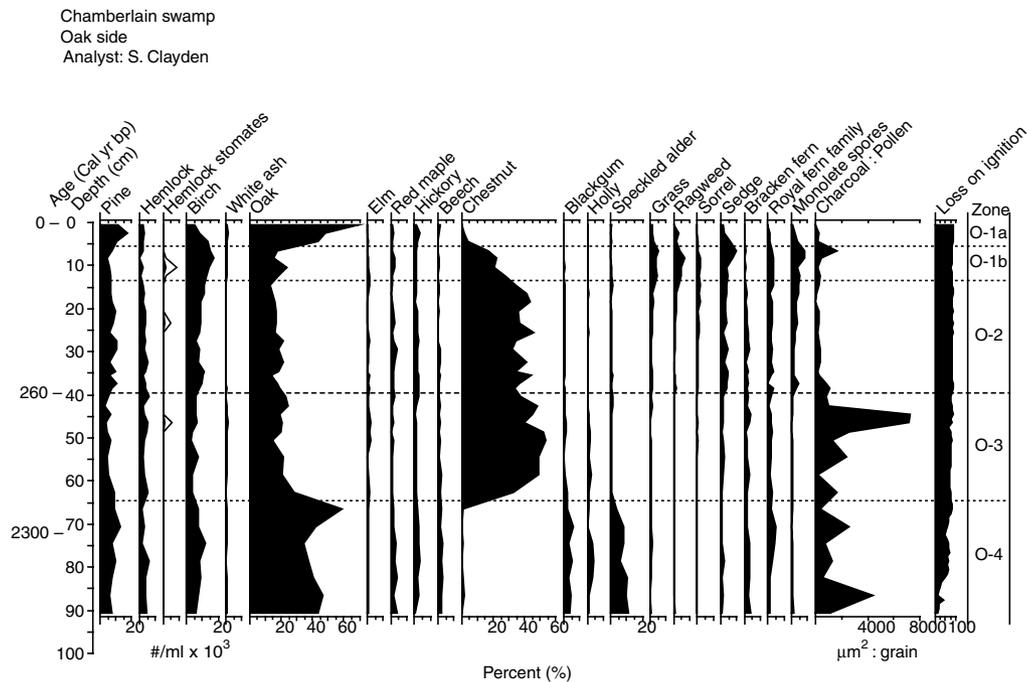


Figure 7 Stratigraphic diagram for the oak (west) side of Chamberlain Swamp depicting changes in pollen and spore percentages, hemlock stomates, charcoal and loss-on-ignition (percent organic material) with sediment depth and age. Four pollen zones were identified objectively using the CONISS clustering results. Zone boundaries correspond to the dramatic rise in chestnut and decline in oak and wetland taxa (O-3 / O-4), European settlement, regional forest clearance and agriculture, and decrease in charcoal (O-2 / O-3), and the historical decline in chestnut (O-1 / O-2). A subzone was identified at *c.* 5 cm that corresponds to the great increase in oak and final decline of chestnut. A few hemlock stomates occur sporadically within the upper 45 cm.

the oak side) and wetland taxa, including black gum, holly and alder. These dynamics resemble those in Lily Pond (zone L-2), however, with a much greater relative abundance of chestnut and more substantial decline in oak. Beech and red maple also decline while birch, hemlock and pine remain relatively stable. On the hemlock side the wetland taxa remain at somewhat higher levels. Charcoal values increase greatly on the hemlock side, but remain lower than on the oak side where they fluctuate and have one major peak at 45-cm depth.

O-2 and H-2. This zone includes the appearance and gradual increase of agricultural weeds indicative of European settlement and regional forest clearance. Chestnut has slightly lower and declining values, oak reaches its lowest value of 8% at the hemlock side and *c.* 15% at the oak side, whereas birch increases through the zone. Charcoal values drop on the oak side, decrease more gradually on the hemlock side and are similar on both sides for the first time.

O-1b and H-1b. This subzone is characterized by the peak in agricultural weeds, an abrupt decline in chestnut and increases in birch and oak. Hemlock and red maple increase on the hemlock side only. Hemlock stomates, which only occur above 30 cm, are consistently present at high and increasing concentrations on the hemlock side. In contrast, they occur discontinuously and at much lower concentrations on the

oak side. With the exception of one small peak on the oak side charcoal values remain low.

O-1a and H-1a. Chestnut declines sharply to <2%, agricultural taxa decline continuously, oak increases greatly especially on the oak side and to levels greater than during pre-European times. Pine increases and birch declines. On the hemlock side hemlock increases to the top and stomate concentrations remain high. Charcoal values remain low.

Multivariate analysis of pollen data

The combined PCA of the pollen data from the oak and hemlock sides depicts long-term changes in pollen assemblages (Fig. 8). Results illustrate the close similarities of the inferred vegetation and its long-term dynamics on the two sides of the swamp through time, but they also highlight the historical divergence that led to the pattern of oak on the west and hemlock on the east side. Specifically, the uppermost samples on the oak side move to ordination space adjacent to samples from Zone O-4 (*c.* 3600–1500 yr BP) in which oak is the dominant taxon, whereas the recent samples from the hemlock side remain distinct because of unusual amounts of hemlock, birch and red maple. In both cases there is a remarkable and similar change from oak to chestnut dominance before European settlement.

Analysis of all pollen samples from fourteen lakes across central Massachusetts and Connecticut displays the changing

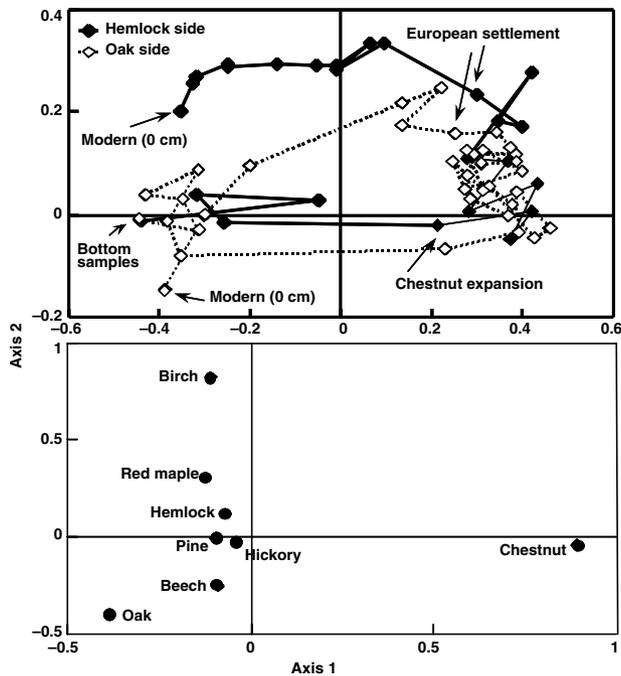


Figure 8 Results of a principal component analysis of the combined pollen percentage data from the oak (shaded) and the hemlock (black) sides of Chamberlain Swamp (see Figs 6 and 7). Results are plotted against the first two principle axes (which explain 91% of the variation), with samples from the two cores (a) and the species loadings, and (b) graphed separately for clarity. Adjacent samples (diamonds) are connected and major periods are indicated, including the bottom samples in both cores, the period of population expansion of chestnut (boundary of zones 3/4) and European settlement (zones 2/3). The overall trajectories and inferred vegetation dynamics from the two records are quite similar through time until the recent period following European settlement. Subsequent to this time samples from the oak side return towards the original composition (i.e. with high values of oak pollen) whereas samples from the hemlock side continue to move into novel positions because of the abundance of birch, red maple, and hemlock and relatively low values for oak.

temporal relationship among pollen assemblages from Lily Pond and other areas (Fig. 10). During the pre-European period many Lily Pond samples have a distinctly separate distribution as a result of the high abundance of chestnut and unusual combination of high oak, beech, hemlock and pine pollen (Fig. 10). During the historical period pollen assemblages from Lily Pond fall within the broad cluster of samples from all sites. Overall, the distribution of samples changes strikingly between these analyses: pre-European samples are clearly spread along the first axis in contrast to historical samples, which form a dense and packed distribution. Relationships between pollen assemblages and climatic parameters (growing degree days) exhibit similar changes. The relationship is slightly stronger ($r^2 = 0.865$ vs. $r^2 = 0.807$) for pre-settlement as opposed to historical samples (Fig. 11). Lily Pond is well off the pre-European regression line, with a pollen assemblage more characteristic of sites with higher

values of GDD. Removal of Lily Pond from the analysis of pre-European samples strengthens the relationships to $r^2 = 0.95$. In all cases the best fit of data occurred between values for PCA axis 1 and growing degree-days calculated for a 5-km radius (vs. 10 or 20 km).

DISCUSSION

A fundamental objective of ecology and conservation biology is to interpret the manner in which broad environmental drivers, local site factors, and disturbance processes interact to control patterns and changes in biotic assemblages at different spatial scales. Judicious use of modern, historical and palaeoecological approaches provides both the lengthy record of vegetation and environmental change and the range of spatial resolution necessary to develop insights into these patterns and processes (Jacobson & Bradshaw, 1981; Clark, 1989; Foster *et al.*, 1996, 2002a,b; McLachlan *et al.*, 2000). In the present study, it is possible to contrast the timing and aspects of stand, landscape and regional forest dynamics, and to relate these to climate change, fire regimes and historical land-use patterns. In addition to illuminating the factors driving vegetation patterns, these results highlight surprising episodes of rapid change between lengthy periods of stable pollen assemblages. The study also underscores the changing importance of fire and humans in this north-eastern landscape over time.

These interpretations are based on our ability to resolve vegetation composition and to infer disturbance processes and environmental drivers at multiple spatial scales by comparing the stratigraphic records from basins of different size, in the context of a regional array of palaeoecological, historical and modern information (cf. Bradshaw, 1988). For example, the sediments at 3-ha Lily Pond should receive pollen predominantly from a 1–10 km radius (cf. Jackson, 1990; Sugita, 1993; Fuller *et al.*, 1998; Jackson & Lyford, 1999). When we analyse these records in conjunction with the network of pollen records from small ponds across southern New England we can examine how the forest dynamics and fire history of the Prescott Peninsula fit within broad-scale gradients of climate, human activity and forest composition (Fuller *et al.*, 1998; Foster *et al.*, 1998b; Francis & Foster, 2001; Parshall & Foster, 2002). Meanwhile stand-level data from the two sides of Chamberlain Swamp portray local differences in forest composition that can be compared with the Lily Pond record to interpret details in stand dynamics and landscape patterns.

Broad-scale vegetation dynamics and controls

The Lily Pond record indicates that over the past few millennia two lengthy (> 1000 years) periods of relatively stable but contrasting forest composition and fire regimes were separated by a brief period of rapid change and followed by the post-settlement period of rapid and ongoing vegetation change (cf. Fig. 5). The major factors controlling these vegetation dynamics appear to be climate during the pre-settlement period and land-use during the post-settlement

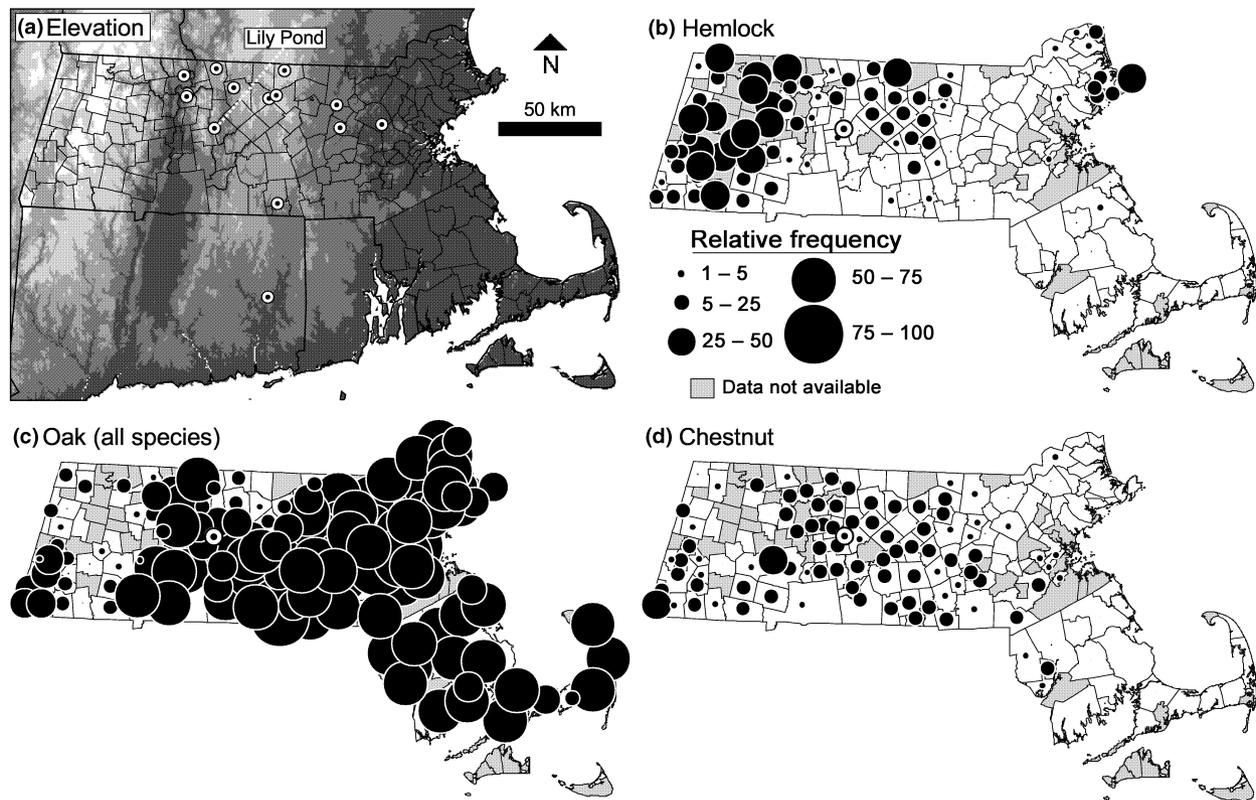


Figure 9 Maps of Massachusetts showing the location of the Lily Pond study area in relationship to (a) topography and the location of other pollen sites used in the regional pollen analysis (see Figs 10 and 11), and (b–d) the abundance of selected tree taxa that are important around Chamberlain Swamp at the time of European settlement. Whereas hemlock (b) had principally a northern and higher elevation distribution, corresponding to its role as a major species in the Hemlock–Northern Hardwood Forest and oak species (c) had a southern, coastal and lower elevation distribution, chestnut (d) was less abundant and had a restricted distribution, confined to the central portion of the state and not extending into south-eastern, coastal Massachusetts. Lily Pond and Chamberlain Swamp occur in an area with relatively high amounts of chestnut, more oak and relatively little hemlock. Data were derived from Proprietors records (boundary surveys) conducted at the time of settlement of each township and are available as unpublished data from the Harvard Forest Archives [see Foster *et al.* (1998b) and Hall *et al.* (2002) for additional information].

period. However, forest composition, climate, and human activity interact with and condition the behaviour of fire, which has been an important, although varying factor throughout time (see Fire, below).

For approximately 2000 years (*c.* 3500–1400 yr BP) Lily Pond pollen assemblages were dominated by oak, with substantially less beech, birch, pine, hickory, hemlock, and sugar maple and low levels of chestnut. Abundances of oak and charcoal greatly exceed those from other pollen records in the New England Uplands (*cf.* Patterson & Backman, 1988; Fuller *et al.*, 1998; Parshall & Foster, 2002), whereas percentages for northern hardwood taxa (beech, birch, sugar maple) and hemlock are much lower (Fuller *et al.*, 1998). In this regard, although Lily Pond is located in the Central Uplands its vegetation and fire history are more similar to records from the lower and warmer Connecticut Valley and Eastern Lowlands (*cf.* Fig. 11; Parshall & Foster, 2002). The southern nature of this pollen assemblage is indicated by its displacement from the regional regression of pollen and

growing degree-days. The consistent but low presence of chestnut pollen since at least 2600 yr BP (and apparently contemporaneously in the two Chamberlain Swamp cores at < 1–10%) suggests that chestnut was scattered throughout the landscape during this period (*cf.* Russell, 1987; Foster & Zebryk, 1993; Paillet, 2002). The major difference between these records is that at the swamp the abrupt shift between chestnut and oak involves a complete change in local forest cover, whereas at Lily Pond the record indicates the persistence of considerable oak within the broader landscape and region.

The rise of chestnut *c.* 1400 yr BP is abrupt and large, especially given the generally under-represented nature of chestnut in the regional pollen rain (*cf.* Foster & Zebryk, 1993; Russell *et al.*, 1993; Paillet, 2002). In the pond and swamp records pronounced changes in upland and wetland vegetation and charcoal are apparent that coincide with the chestnut rise, and are interpreted as driven by broad-scale climate change (*cf.* Parshall *et al.*, 2003). However,

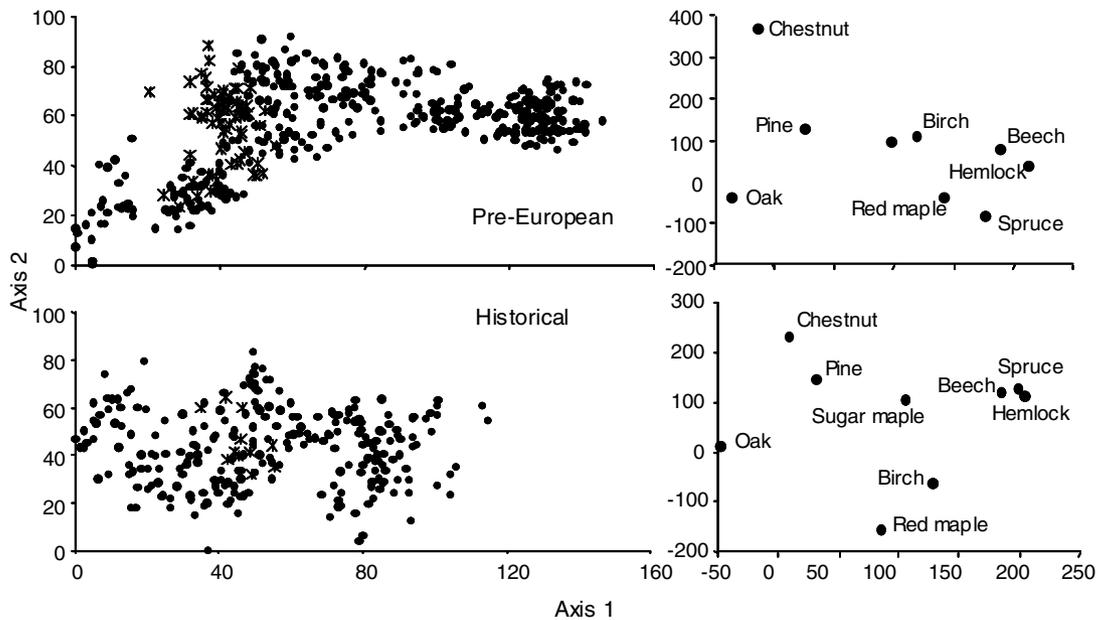


Figure 10 Detrended correspondence analysis of upland tree pollen data from thirteen lake sediment stratigraphies distributed across Massachusetts and Connecticut, showing the relationship among samples from the pre-European period (c. 1000–260 yr BP; top) and historical period (260 yr BP to present; bottom). In general, there is considerably less separation and spread among sites during the historical period than before, as a consequence of more regional similarity in pollen assemblages and inferred vegetation (cf. Foster *et al.*, 1998b; Fuller *et al.*, 1998). Data are unpublished from the Harvard Forest Archives and methods follow Fuller *et al.* (1998).

determining the exact nature of this shift is problematical as it is accompanied by confounding changes in vegetation and charcoal, and may be influenced by human activity. In particular, there is a decline in wetland trees and shrubs (black gum and alder) and *Sphagnum* moss, an increase in shallow-water aquatic species (waterlilies and *Isoetes*), an increase in sweet gale (*Myrica-Comptonia*), and an increase in the organic content of the sediment. These changes appear to reflect an increase in moisture availability and rise in the water-table, leading to the flooding of marginal wetlands and development of deeper water and bordering mats of *Myrica*. This interpretation is consistent with the rise in hemlock and chestnut, mesic species and a rise in ground water tables in northern New England (Almquist *et al.*, 2001). However, charcoal delivery to the lake sediments approximately doubles when chestnut increases suggesting either a shift in fire regime to increasing frequency or size of fires or an increased production and transport of charcoal under a different vegetation.

Regional climate change after 2000 yr BP has been identified in other north-eastern USA studies and is variously associated with gradual increases in spruce (Davis *et al.*, 1980; Schauffler & Jacobson, 2002), chestnut (Davis, 1969; Spear & Miller, 1976; Whitehead, 1979; Paillet, 1982; Russell, 1987), and other taxa. Although most researchers identify this event as a pronounced cooling trend (cf. Davis *et al.*, 1980), the enigmatic and coincident increases in northern (spruce) and southern (chestnut) taxa have left the specific nature of this complex environmental change unclear (Rus-

sell, 1987; Schauffler & Jacobson, 2002). The current study suggests that moisture availability and fire also change during this period. The three records also indicate that the change may have been quite rapid (cf. Parshall *et al.*, 2003).

Stand dynamics and the development of landscape patterns

When compared with the Lily Pond stratigraphy the two Chamberlain Swamp records allow us to examine stand and landscape-level changes within the context of broader forest dynamics. The local records closely parallel the broad-scale Lily Pond record and therefore we interpret the major dynamics at all scales to be controlled by the same broad-scale processes: climate change and land use. Whereas the stratigraphy at Lily Pond homogenizes pollen signals from many different stands across the Prescott Peninsula, the distinctive swamp records reflect more local environment and forest history. In particular, the pollen percentages for chestnut during the millennium before European settlement are consistently higher at the swamp (>30%) than in any lake records from this or other regions (cf. Russell, 1987; Fuller *et al.*, 1998; Paillet, 2002).

Presumably, the two local records are similar because of similarity in forest cover around the swamp until after European settlement and overlap in their pollen source areas (Sugita, 1993; Jackson & Lyford, 1999). Both document two lengthy (millennial) periods of relatively stable forest composition connected by a brief period of rapid change. This

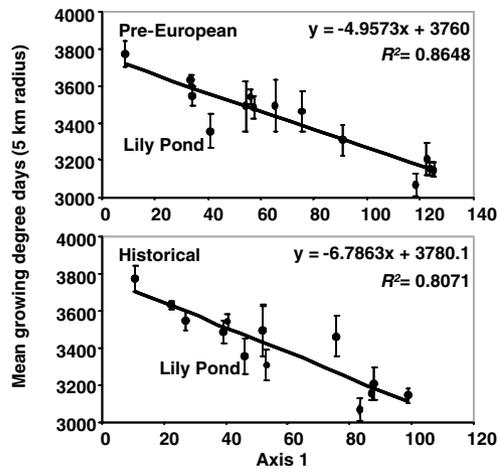


Figure 11 Relationship between climate (growing degrees days) and pre-European vegetation composition in southern New England as inferred from pollen analysis of thirteen lake sediment stratigraphies in southern New England (see Fig. 9 for site locations). Analysis represents the linear regression of the centroid for each site's samples on the first DCA axis against growing degree days for the area within 5 km of the site, as calculated according to Ollinger *et al.* (1990). Whereas the site distributions form an overall strong relationship with climate, the samples from Lily Pond are furthest removed from the regression line. The regression relationship is improved from $r^2 = 0.86$ to 0.95 when the samples from Lily Pond are removed. In all cases a 5-km radius for climate provided a better fit with the data than 10 or 20 km.

result indicates that forests may maintain single species dominance over long periods of time (e.g. oak from at least 3500 yr BP until 1500 yr BP, chestnut from 1500 to 240 yr BP) and even when, or perhaps as a result of being, subjected to fairly frequent disturbance. High charcoal concentrations in the records suggest that fire occurred throughout both periods, although most likely at varying frequencies. Independent reconstructions of the regional hurricane regime also suggest that exposed sites like the Prescott Peninsula are subjected to episodic, severe wind impact (Boose *et al.*, 1993, 2001).

Although the two records display similar and synchronous dynamics over the first 2000 years, they diverge strongly in composition since European settlement, as the hemlock side exhibits higher values for birch, red maple, and hemlock pollen, and hemlock stomates (Figs 6 and 7). Consequently, the modern landscape pattern of oak on the west side and hemlock on the east side of Chamberlain Swamp appears to be initiated by changes associated with human land use. In particular, historical records indicate that the entire area was heavily logged, although never cleared, and the sedimentary records suggest that there was a major decline in local fire activity following European settlement.

The low values for hemlock pollen and absence of hemlock stomates throughout the pre-settlement record suggest that hemlock was not present in forests immediately adjacent to the swamp during that time (Parshall, 2002). We

infer that hemlock was excluded by fire from the broad upland ridge where it is growing and establishing today (Nichols, 1913; Winer, 1955; Niering *et al.*, 1970; Foster & Zebryk, 1993). During the pre-European period hemlock may have occupied the rocky slopes extending down to the valley floor (Fig. 2). The increase in pollen and appearance of hemlock stomates in the late nineteenth century indicate the establishment of the hemlock forest on the eastern side of the swamp. Development of this landscape pattern may have been promoted by the local decline in fire that occurred with European settlement, coupled with the decline in chestnut (Merrill & Hawley, 1924; Paillet, 1982, 2002).

Subtle differences do exist between the uplands on either side of the swamp, in particular the oak side is drier and rises more rapidly up from the swamp, whereas the hemlock side has a low and moist border and rises less steeply. The hemlock side is also slightly protected by the wetland from surface fires driven by prevailing westerly winds. Although intense fires in dry years probably burned across or around the swamp, the east side would have experienced a lower incidence of fire than the west side, which is a continuation of the broad ridge of the Prescott Peninsula. During pre-settlement times this difference in fire regime and site conditions probably accounts for the slight difference in pollen assemblages and charcoal abundance, including consistently higher charcoal values, higher values for oak, hickory and chestnut and lower values for wetland taxa on the oak (west) side. Thus subtle differences in environment and fire susceptibility on opposing sides of the narrow swamp may have led to differential change with the advent of land use, a decrease in fire and the loss of chestnut.

Dynamics of chestnut

The history of chestnut, as revealed by the local (Chamberlain Swamp), landscape (Lily Pond) and regional historical records (Foster *et al.*, 1998b; Fuller *et al.*, 1998) provides general insights as well as details concerning this important tree species. When palaeoecologists examine the post-glacial migration of species they attempt to identify the first arrival of a species at low abundance and distinguish this from later periods of abundance (Davis *et al.*, 1980; Parshall, 2002). In essence this is a problem of separating the 'true' migration from the subsequent 'appearance' of migration when the taxon's population size increases (Huntley & Webb, 1989). Chestnut provides an example of the importance of making this distinction because its post-glacial movement up the East Coast is remarkably slow in relation to other temperate species. There remain major questions concerning this delay and whether it is real or apparent (Russell, 1987; Paillet, 2002). Chestnut is insect-pollinated and its pollen is released after leaf-out; therefore, it is poorly dispersed and under-represented in the pollen record (Murdock, 1912; Russell, 1987).

Although a single study from Massachusetts does not resolve all issues, both the local and regional records from the Prescott Peninsula indicate that chestnut pollen occurred at low levels and that the species was present well before its

major expansion *c.* 1500 yr BP. Apparently, it migrated into the area, became established at low abundance and subsequently developed into a major component of this landscape after broad-scale environmental change. As the population increased the species became widely apparent in the stratigraphic records (cf. Paillet, 2002).

The abrupt increase in chestnut at *c.* 1500 yr BP raises questions concerning the mechanisms by which it rapidly increased in an established forest dominated by a long-lived species like oak (cf. Jacobson, 1979). The explanation may involve chestnut's long-term and presumably widespread presence in the landscape, its ability to disperse seeds effectively and establish shade-tolerant seedlings at a large distance from source populations, and its prolific sprouting after disturbance (Paillet *et al.*, 1989; Billo, 1998). Although the chestnut blight handicaps our ability to explore the biology of chestnut (Paillet, 1982, 2002), Henry Thoreau's extensive nineteenth century observations on the growth, seed dispersal and seedling distribution of chestnut in Massachusetts forests provides key insights into its ability to spread into forested areas (Foster, 1999).

Looking through this wood and seeking very carefully for oak seedlings and anything else of the kind, I am surprised to see where the wood was chiefly oak a cluster of little chestnuts six inches high and close together...I was surprised at the sight of these chestnuts, for there are not *to my knowledge* any chestnut trees – none, at least, nearly large enough to bear nuts – within about half a mile of that spot...and yet from what I saw then and afterward I have no doubt that there were hundreds, which were placed there by quadrupeds and birds' (H.D. Thoreau, 17 October 1860; Foster, 1999).

Once established, chestnut seedlings and sprouts are quite shade tolerant and can rapidly enter the canopy as the overstorey opens through tree mortality by fire, windthrow or cutting (Paillet, 1984, 2002). Intense fires thin an oak canopy and large overstorey oaks generally do not resprout after fire (Abrams, 1992, 1996; Del Tredici, 2001). However, smaller hardwood seedlings and understorey trees do sprout, especially chestnut, which is one of the most effective sprouting and rapidly growing north-eastern trees (Paillet, 1984; Foster & Zebryk, 1993; Del Tredici, 2001). In the pollen records from Chamberlain Swamp and Lily Pond the rise in chestnut is associated with an inferred climate change and increase in charcoal abundance. Under favourable conditions for establishment and growth and an active disturbance regime, chestnut could rapidly increase from a well-dispersed but small population.

The relative importance and role of chestnut in the pre-European landscape of New England is poorly known (but cf. Cogbill *et al.*, 2002; Hall *et al.*, 2002; Paillet, 2002). Some studies document an increase in chestnut in the eighteenth and nineteenth centuries as a result of sprouting after fire and repeated cutting, leading to suggestions that chestnut abundance was an artefact of human activity (Russell, 1987; Foster *et al.*, 1992; Foster & Zebryk, 1993; McLachlan

et al., 2000). This study suggests that chestnut did play a major role over a millennial period before European settlement in some forests. Witness tree data confirm that chestnut comprised 5–25% of the trees tallied in many individual townships at the time of European settlement (Fig. 9). Notably, its abundance was generally less than that of oak and it was important in a more restricted area in the south-central portion of Massachusetts. The pollen records also suggest that the 1500-year abundance at Lily Pond was not typical of sites to the north or east.

The local decline of chestnut near Chamberlain Swamp following European settlement occurs in three stages. Coincident with settlement and the initial rise in agricultural weeds there occurs a slight decrease in chestnut pollen paralleled by a decline in fire (charcoal values) and slight increase in birch and then red maple and hickory. There are at least two possible explanations for this pattern. A minor change in forest composition from a decline in fire frequency might occur because of extirpation of the Native American population, a possible ignition source. Alternatively, declining fire might result from cooler, moister conditions associated with the Little Ice Age (*c.* 1450–1850 AD; Gajewski, 1987, 1988; Jones & Bradley, 1992; Baron & Smith, 1996; Fuller *et al.*, 1998). We infer that the species involved are black and yellow birch, which are present throughout the upland and the swamp and are more shade tolerant than paper or grey birch.

A second, greater decline in chestnut occurs *c.* 1850 AD as land clearance and land-use intensify. As this decline is not mirrored at Lily Pond it is interpreted as a stand-level phenomenon resulting from intensive human impact on the forests right around Chamberlain Swamp. Although a decline of chestnut with intense land use contradicts some studies (cf. Foster *et al.*, 1992; McLachlan *et al.*, 2000) it is supported by contemporary observations and the trajectory of wood utilization. At this time forest area was at a historical low and many sources indicate that cutting of remaining woodlots for timber, fuel and the growing railroad industry was intensive (Frothingham, 1912; Williams, 1982; Whitney, 1994; Foster, 1999). As chestnut was a preferred species it is reasonable that it was heavily cut, leading to its decline and an increase in less-preferred, species. Indeed a contemporary account by Henry Thoreau documents a sharp decline in chestnut from exactly this cause.

It is well known that the chestnut timber of this vicinity has rapidly disappeared within 15 years, having been used for railroad sleepers, for rails and for planks, so that there is danger that this part of our forest will become extinct. (H.D. Thoreau, 17 October 1860; cf. Foster, 1999).

In addition to selective cutting Thoreau mentions nut collection as a cause for local decline in chestnut. Chestnuts and their seedlings are also heavily eaten by cattle, which frequently grazed nineteenth century woodlots (F. Paillet, pers. comm.).

The final, precipitous decline of chestnut in the Chamberlain Swamp records occurs because of the chestnut blight around 1913 (cf. Korstian & Stickel, 1927). Thus, over the past 300 years chestnut has undergone three declines, each related to land-use but differing in cause, specifics, and associated vegetation dynamics.

Fire history and role in vegetation patterns

Discussion and debate over the role, cause and variability in fire activity in the north-east have proceeded over the last 50-years, with no sign of abating (cf. Day, 1953; Pyne, 1982; Cronon, 1983; Russell, 1983; Clark *et al.*, 1996; Abrams & Seischab, 1997). The present study provides the first detailed evaluation of fire in the Uplands of south-central New England within the region dominated by oak and other hardwoods (cf. Parshall & Foster, 2002). The results indicate that fire was a recurrent disturbance over the past 3500 years and may be a critical factor in understanding long-term vegetation pattern and dynamics.

Charcoal values in the three cores are among the highest for central Massachusetts and New England, outside the sandy, coastal areas of Martha's Vineyard (Backman, 1984; Patterson & Backman, 1988; Stevens, 1996; Foster & Motzkin, 1998; Parshall & Foster, 2002). At all sites charcoal values change in major ways with inferred environmental and vegetation change and with the onset of European settlement and land-use activity. Initial values are high at Lily Pond and the oak side of Chamberlain Swamp during the period of oak dominance (*c.* 3500–1500 yr BP). They then rise substantially with the increase in chestnut and with the inferred increase in moisture availability. These data fit well with a strict interpretation that fire frequency is largely controlled by climate, although the direction of change towards more fire is not consistent with the interpretation of cooler, moister conditions. However, the leaf litter and fine fuels in chestnut forests differ substantially from those in oak forests and may trigger feedbacks between the vegetation and fire regime. Another alternative, is that coincident with the change in environment and vegetation that there was a change in the behaviour pattern of Woodland Indians, a potential ignition source for fire (Bragdon, 1996). If Indian-set fires were not just escaping from lowland sites or accidental ignitions but were purposefully set to manipulate the woodland environment, then this hypothesis is clearly tenable (M. Mulholland, pers. comm.).

Although uncertainty persists in terms of causal connections, the study indicates that in two very different sedimentary basins there are coincident changes in climate, vegetation and fire activity. Interestingly these results broaden and confound the debate on the role or necessity of fire in the maintenance and development of oak in eastern temperate forests (cf. Abrams & Seischab, 1997; Clark, 1997; Delcourt *et al.*, 1998; Ison, 2000). The data corroborate other results from New England suggesting that fire may be associated with oak and is important in oak forests (Brown, 1960; Niering *et al.*, 1970; Foster *et al.*, 1998a;

Fuller *et al.*, 1998; Orwig *et al.*, 2001). However, they also indicate that an increase in fire activity was associated with a shift from oak to chestnut dominance. In the post-European landscape and especially within the last century oak dominance across the Prescott Peninsula seems to have been favoured and maintained by heavy cutting in an era of relatively low fire activity and the elimination of chestnut as a competing species.

These results are compatible with the conclusion that fire was an important but varying force shaping vegetation patterns at the regional, landscape and stand scale in central New England (Patterson & Backman, 1988; Fuller *et al.*, 1998; Parshall & Foster, 2002). Given that fire ignitions are inferred to be largely anthropogenic in origins this also implies that the New England landscape must be considered controlled, at least in part, by cultural, as well as natural and environmental factors over past millennia. The rationale for this assertion is based on three observations: (i) high charcoal values indicate that fire was an ongoing active process; (ii) inferred fire activity changed with vegetation changes and cultural dynamics; and (iii) the two species that predominate in the landscape over the last 3500 years, oak and chestnut, are moderately shade-tolerant, long-lived, sprouting and fire-tolerant species that appear to require disturbance to be maintained at high abundance levels. Consequently, with a major decline in fire mesic, shade-tolerant but fire intolerant species like hemlock and red maple can gradually increase (Patterson & Backman, 1988; Lorimer, 1989).

CONCLUSIONS

By taking a long-term perspective on vegetation dynamics that includes a range of spatial scales we begin to appreciate the complex processes involved in the development of modern ecological patterns. The ridge of the Prescott Peninsula is covered with an extensive, mature oak forest with a restricted patch of hemlock and little apparent evidence of chestnut. And yet, the area was once dominated by chestnut, the hemlock stand is apparently supporting its first generation of trees, and fire – an important though infrequent disturbance in the history of the area – has not occurred in over 100 years. Although the long-term history of the forests is marked by remarkable stability, this dominance by a single species or genus appears to be facilitated and maintained by disturbance. Transitions between these forest types were driven by environmental changes recorded at a local and regional scale. Meanwhile, the two dominant species in the area's history – oak and chestnut – have decidedly different distributions and histories across the larger New England area.

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BIOSKETCHES

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Susan Clayden is a palynologist currently finishing her PhD at the University of New Brunswick who has undertaken paleoecological studies in New England, Canada, and Siberia.

David A. Orwig is a forest ecologist interested in dendroecology and the role of land use history and disturbance on forest dynamics. His current research integrates community, landscape and ecosystem approaches in examining the ecological consequences of an invasive insect pest in hemlock forests of New England.

Brain Hall is a graduate of the State University of New York (SUNY) at Plattsburgh and SUNY College of Environmental Science and Forestry in Syracuse, New York. He is a research assistant at the Harvard Forest specializing in GIS-based analysis and data presentation. His work allows him to combine his background in plant ecology with his lifelong interest in the cultural history of New England.

Sylvia Barry is a graduate of the University of California, Santa Cruz, and the University of Minnesota. She is a researcher in palaeolimnology at the Harvard Forest investigating the response of forest ecosystems to past climate change.

Appendix I Pond sites from Central Massachusetts and Connecticut used in DCA analysis

Site	Reference	Longitude	Latitude	Elevation (m)	Size (ha)
Aino	Fuller <i>et al.</i> 1998	-71.9255	42.6808	354	1.7
Bates	Foster <i>et al.</i> unpub.	-72.0162	41.6588	95	2.7
Blood	Foster <i>et al.</i> unpub.	-71.9615	42.0800	214	8.5
Green	Fuller <i>et al.</i> 1998	-72.5111	42.5668	80	5.4
Lake Pleasant	Fuller <i>et al.</i> 1998	-72.5138	42.5597	80	21.9
Lily. New Salem	Foster <i>et al.</i> unpub.	-72.3468	42.4181	303	2.3
Lily. Warwick	Fuller <i>et al.</i> 1998	-72.3366	42.6881	269	0.8
Little Mirror	Fuller <i>et al.</i> 1998	-71.6090	42.5254	73	2.4
Little Bolton	Fuller <i>et al.</i> 1998	-71.5877	42.4223	99	7.0
Otter	Fuller <i>et al.</i> 1998	-72.5331	42.6555	107	2.0
Quag	Fuller <i>et al.</i> 1998	-71.9568	42.5674	332	0.4
Silver	Fuller <i>et al.</i> 1998	-72.2294	42.6009	161	4.1
Snake	Fuller <i>et al.</i> 1998	-72.0170	42.5559	282	2.4
Walden	Foster <i>et al.</i> unpub.	-71.3380	42.4391	50	24.9