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The forests of presettlement New England, USA: spatial and compositional patterns based on town proprietor surveys

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Abstract

Aim This study uses the combination of presettlement tree surveys and spatial analysis to produce an empirical reconstruction of tree species abundance and vegetation units at different scales in the original landscape.

Location The New England study area extends across eight physiographic sections, from the Appalachian Mountains to the Atlantic Coastal Plain. The data are drawn from 389 original towns in what are now seven states in the north-eastern United States. These towns have early land division records which document the witness trees growing in the town before European settlement (*c.* seventeenth to eighteenth century AD).

Methods Records of witness trees from presettlement surveys were collated from towns throughout the study area (1.3×10^5 km^2). Tree abundance was averaged over town-wide samples of multiple forest types, integrating proportions of taxa at a local scale (10^2 km^2). These data were summarized into genus groups over the sample towns, which were then mapped [geographical information system (GIS)], classified (Cluster Analysis) and ordinated [detrended correspondence analysis (DCA)]. Modern climatic and topographic variables were also derived from GIS analyses for each town and all town attributes were quantitatively compared. Distributions of both individual species and vegetation units were analysed and displayed for spatial analysis of vegetation structure.

Results The tally of 153,932 individual tree citations show a dominant latitudinal trend in the vegetation. Spatial patterns are concisely displayed as pie charts of genus composition arrayed on sampled towns. Detailed interpolated frequency surfaces show spatial patterns of range and abundance of the dominant taxa. Oak, spruce, hickory and chestnut reach distinctive range limits within the study area. Eight vegetation clusters are distinguished. The northern vegetation is a continuous geographical sequence typified by beech while the southern vegetation is an amorphous group typified by oak.

Main conclusions The wealth of information recorded in the New England town presettlement surveys is an ideal data base to elucidate the natural patterns of vegetation over an extensive spatial area. The timing, town-wide scale, expansive coverage, quantitative enumeration and unbiased estimates are critical advantages of proprietor lotting surveys in determining original tree distributions. This historical–geographical approach produces a vivid reconstruction of the natural vegetation and species distributions as portrayed on maps. The spatial, vegetational and environmental patterns all demonstrate a distinct 'tension zone' separating 'northern hardwood' and 'central hardwood' towns. The presettlement northern hardwood forests, absolutely dominated by beech, forms a continuum responding to a complex climatic gradient of altitude and latitude. The oak forests to the south are distinguished by non-zonal units, probably affected by fire. Although at the continental scale, the forests seem to be a broad transition, at a finer scale they respond to topography such as the major valleys or the northern mountains. This study resets some preconceptions about the original forest, such as the overestimation of the role of pine, hemlock and chestnut and the

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underestimation of the distinctiveness of the tension zone. Most importantly, the forests of the past and their empirical description provide a basis for many ecological, educational and management applications today.

Keywords

Historical ecology, New England, northern hardwood forest, plant biogeography, presettlement vegetation, proprietory town, surveyor's records, witness tree, vegetation classification, tension zone.

INTRODUCTION

Starting in 1620, settlers from Europe profoundly changed the supposedly 'infinite' woods of New England (Cronon, 1983). By 1850, the land in the current states of Connecticut, Rhode Island, Massachusetts, Vermont and New Hampshire had been completely settled and more than 60% of the land over the entire region cleared for agriculture (Harper, 1918). Areas remaining in forest, mostly on shallow soils, steeper slopes or low-productivity land, were being relentlessly harvested for timber by settlers and businessmen (Williams, 1989). Thus by the middle of the twentieth century, virtually the entire forest had been altered by human activities (Whitney, 1994).

Today less than a small fraction of 1% of the forest in the north-eastern United States remains as a few fragmented scraps of 'old-growth' landscape (Davis, 1996). Although reconstruction of the nature of the presettlement landscape is severely hampered by the lack of modern analogues, several approaches can be used to infer the nature of historical forests by extrapolating from modern data (Whitney, 1994; Russell, 1997; Egan *et al*., 2001). For example, much of New England is (re)forested today and it has been posited that the 'recovered' vegetation appears similar to the forests before 1775 (MacCleery, 1992). Moreover, several proxies of the ostensibly original forest have been drawn from different sources: 'virgin' remnants (e.g. Nichols, 1913; Cline & Spurr, 1942; Braun, 1950); successional tendencies and silvicultural experience in managed stands (e.g. Hawley & Hawes, 1912; Westveld *et al*., 1956); and theoretical models of forest development and response to the environment, particularly climate (e.g. Weaver & Clements, 1938; Bormann & Likens, 1979; Pacala *et al*., 1993). Yet each of these approaches has its limitations. 'Remnant' stands, by definition, have escaped expected natural disturbances and are atypical of the 'common' landscape at any time. The few uncut stands are a limited and selective spatial sample and survived exactly because they have unusual histories or extreme settings (Cogbill, 1996). Predictable physiological and silvicultural responses are dependent on temporal continuity and stable environmental conditions, which are constrained by species migrations, climate changes and soil development in glaciated regions (Russell, 1997). Models tend to be simplistic, deterministic and linear expressions of a few common stereotypes. Thus the current vegetation in New England is potentially a biased evidence of the past and the common surrogates of past forests have questionable applicability in quantifying forest vegetation before settlement.

Altogether inferential methods, such as modern vegetation, ecological models, and/or theoretical relationships to environment are problematic in determining a spatially comprehensive and temporally accurate view of the historic forest of New England. There are, however, empirical observations which describe the forests of the time. These historical data can also be used to test the accuracy of surrogate inferences. Contemporary observations of explorers, naturalists, diarists, authors and publicists abound, although they are subjective, limited in coverage and typically qualitative (Whitney, 1994; Russell, 1997; Bonnicksen, 2000; Edmonds, 2001). Significantly, the classical syntheses of the native vegetation across New England (e.g. Nichols, 1913; Bromley, 1935; Cline & Spurr, 1942; Braun, 1950; Westveld *et al*., 1956; Bormann & Buell, 1964) are based on a combination of anecdotal accounts, together with sampling in the last putative remnants and intensive field knowledge of the existing vegetation. Interestingly, despite explicitly linking these proverbial inferences (variously called 'natural', 'virgin', 'climax', 'original', 'primeval' or 'old-growth' forests) to the past, none of these studies compare their theorized species composition or pattern of forest types with actual historical data.

Fortunately, a spatially comprehensive and temporally relevant representation of past vegetation is contained in the land division surveys carried out in anticipation of European settlement. In the Midwest, the United States General Land Office (GLO) surveys have long been the primary resource for hundreds of studies of the historical landscape, and several states have recently digitized their entire survey database (Whitney, 1994; Whitney & DeCant, 2001). These federal surveys typically include descriptions of general species composition, changes in community units and reference to blazed trees marking predetermined points at intervals along the survey lines (e.g. Bourdo, 1956; White, 1984; Manies & Mladenoff, 2000). In contrast, in colonial New England and later in the original states, town-mediated surveys regularly cited only 'witness' trees. These unregulated and unstandardized eastern surveys have received relatively little interest, perhaps because they are obscure and are found in widely scattered repositories (e.g. McIntosh, 1962; Russell, 1981; Loeb, 1987; Seischab, 1990; Marks & Gardescu, 1992; Abrams & Ruffner, 1995; Cowell, 1995; Abrams & McCay, 1996; Cogbill, 2000; Black & Abrams, 2001). In New

England, case studies have analysed the presettlement composition for selected sections of Vermont (Siccama, 1963, 1971), Maine (Lorimer, 1977) and Massachusetts (Foster *et al.*, 1998; Burgi & Russell, 2000). In addition, Whitney (1994) has collated data from 145 presettlement surveys documenting witness trees across the northeast quarter of the United States and produced isopleth contour maps of equal presettlement abundance ('isowits') for fourteen taxa. These include data from seventeen studies representing twenty-five separate sites from New England and they display coarse zonal distributions on a continental scale.

Town proprietor surveys

In the eighteenth century, a distinctive land tenure system, the proprietory town, arose in the northern English colonies of North America (Clark, 1983; Price, 1995). The colonies, or later states, granted unsettled land in the form of regularly shaped 'towns', typically 6-mile square, to absentee groups of individuals. The work of this business 'proprietorship' was threefold: to divide the commonly held land into individual lots; to locate and mark those lots by a survey; and then to get settlers to move onto the lots and 'improve' them (Woodard, 1936). This sequence resulted in an unintended objective sample of the landscape before European settlement. Archived land division records, primarily lotting surveys citing 'witness' trees as permanent markers of the corners of small lots (1–160 acre; 0.5–65 ha), are available in many of the proprietory towns across the northeast (Whitney, 1994; Whitney & DeCant, 2001). Surveys of individual lots in the earlier granted towns of southern New England and the grants/patents/tracts/manors of New York share many of the same basic characteristics: placement of samples regularly across the town; marked trees to 'witness' lot corners or town divisions and a regular record in archival documents (Foster *et al.*, 1998; Cogbill, 2000).

The available New England lotting surveys date from just after the first established English settlement (1620) to after the Erie Canal (1825) enabled midwestern expansion. The first towns on the coast and in the Connecticut Valley typically tended not to cite witness trees, and some were surveyed before 1700 when citation became a consistent practice (Price, 1995). The frontier moved into the interior during the eighteenth century, but settlements were limited to the southern regions (roughly to the northern boundary of Massachusetts) until the end of the French and Indian Wars in 1763 (Clark, 1983). Northern New England towns were surveyed from *c.* 1770–1810. Some tracts in the northern mountains were never settled, but were granted as late as 1850. Although some surveys, especially in the southern coastal towns, were done after settlement began, the surveys overwhelmingly represent the undisturbed vegetation as European settlement proceeded through towns in the eighteenth century.

Lotting surveys of individual towns were usually completed quickly (i.e. 1–10 years), but the overall vegetation was sampled over a shifting period (1620–1850) spanning more than 200 years. Furthermore, the surveys were spatially transgressive, regularly progressing from the southern coast to the northern uplands. Therefore, spatial patterns could be confounded as a result of parallel, but variable temporal trends in forest conditions. The climate and natural disturbance regimes, such as hurricane occurrence, however, do not show obvious temporal trends across either the two century sampling period or the previous century of tree growth leading into it (Jones & Bradley, 1992; Boose *et al.*, 2001). Culturally during this period aboriginal populations were drastically reduced and indirect European activities, such as the fur trade and its effect on animal populations, were far-reaching. Nevertheless, the inherent longevity of trees and the relative remoteness of the woods insulated the forest itself from most anthropogenic influences. Significantly the processes that most affect the forest (i.e. clearing, logging, grazing, setting of fires) were very localized and closely tied to either indigenous or European settlement activities (Cronon, 1983; Whitney, 1994; Russell, 1997). Therefore, during the majority of the time over most of the study area there was minimal human disturbance before European settlement (Day, 1953). Nevertheless, coastal locations with the largest initial aboriginal populations were generally surveyed close to the time of maximum indigenous influence (Cronon, 1983). In addition, in this study, any effects of the native inhabitants are explicitly considered to be part of the 'original' pattern. Thus the timing of the survey sample is linked to the consistent conditions just before European settlement and represents a narrow spatial-temporal window, herein simply called 'presettlement'.

Vegetation structure

Vegetation patterns are a kaleidoscope of units which become more generalized as the resolution scales up from the tree species and their composition within a single community ($c.10^{-2}$ km^2 extent), through the regional assemblages of those communities in a landscape ($c.10^2$ km^2 extent), to groupings of those landscapes by similar physiognomy or constituent flora ($c.10^5$ km^2 extent). This nested hierarchy of plant community units can be loosely termed the 'community type', the 'association', and the 'formation', respectively (Whittaker, 1975; Delcourt *et al.*, 1983; Poiani *et al.*, 2000). The change in scale typically balances increasing variability and extent with decreasing detail and taxonomic specificity as the scale of resolution decreases (Turner *et al.*, 2001). Significantly, most geographical studies focus on broad-scale patterns among vegetation formations or species ranges, while ecological studies deal with the fine-scale patterns among types. The typical town-size sample already averages tree abundance over multiple forest types, and is thus an ideal scale to reflect the local proportion of trees, as well as species variation at the association scale (Delcourt & Delcourt, 1996).

The distinctiveness of the vegetation in the New England forest likewise depends on the scale of resolution. At a continental scale, plant geographers have traditionally viewed the region as reflecting a gradual transition between climatic 'biomes' or floristic 'provinces', blending the northern coniferous forest with the southern deciduous forest (Merriam, 1898; Gleason & Cronquist, 1964; Bailey, 1996). At an increased resolution, the vegetation of the northeastern United States has been viewed either as a distinct transitional 'formation' supporting a suite of endemic species (e.g. white pine, yellow birch, red spruce and hemlock) or as a pair of distinct 'associations' (i.e. Hemlock–White Pine–Northern Hardwoods and Oak–Chestnut or variously Oak–Hickory) within the deciduous forest formation (Nichols, 1935; Weaver & Clements, 1938; Braun, 1950; Jorgensen, 1971; Vankat, 1979; Delcourt & Delcourt, 2000). At the finest scale, plant ecologists generally find the land covered with a mosaic of individual community types responding to site-specific history or discrete site factors, such as topography, soil or geology (Siccama, 1971; Poiani *et al.*, 2000; Thompson & Sorenson, 2000).

Although the vegetation of New England is composed of both discrete forest types and a blending of zones, there has been no agreement on the position or width of any vegetational boundaries in the region (e.g. Hawley & Hawes, 1912; Bromley, 1935; Braun, 1950; Westveld *et al.*, 1956; Kuchler, 1964; Keys *et al.* 1995). Some of the uncertainty in the vegetation structure is because of its obfuscation by pervasive land use, but also important is the nature of transitions or 'ecotones' in a region of continuous forest (Weaver & Clements, 1938; Gosz, 1991). Although there are seldom discontinuities between higher order vegetation units (e.g. associations), in some cases, such as the transition between the prairie oak woodlands and northern hardwoods forest in Midwest, there is a narrow zone where distinct floristic provinces overlap and multiple species reach their range limits (Clements, 1905; Curtis, 1959; Grimm, 1984; Neilson, 1991). Curtis (1959) named this ecotone the 'tension zone' in Wisconsin. Because of the gentle and continuous geographical gradients, he associated the relatively sharp landscape boundary with climatic variables. Given the similar meeting of floristic provinces in New England, including the southern boundary of the same northern hardwood forest, the presence and location of such an ecotone, albeit abutting another forest type, is of particular interest.

Objectives

Despite a 200-year hiatus since the surveyors' initial collections, the contemporary quantitative sample of the forests of New England before European settlement has not been comprehensively analysed. Therefore, this study compiles and analyses witness tree tallies from available town-wide surveys in order to produce a spatial representation of species distributions and abundances across the region. The primary objective is to use the combination of town proprietor surveys and spatial analysis to produce an empirical reconstruction of the vegetation structure within the presettlement forests. This application of the historical–geographical approach is an ideal opportunity to document the vegetation at both a time (before confounding land use) and spatial scale (landscape) heretofore unavailable. Secondarily, by classifying the assemblages of species it identifies landscape patterns at various scales, including the potential presence of ecotones between adjacent vegetation associations. Finally, by correlating the composition of the vegetation with factors of the physical environment, this study investigates the influence of physical factors upon species and vegetation distribution at a regional scale before any recent changes in climate.

MATERIALS AND METHODS

Study area

A dense network of similarly sized towns from a contiguous area between the Androscoggin River in Maine and the Hudson River in New York have archived presettlement surveys (Fig. 1). This study area is herein broadly termed 'New England', although this term traditionally encompasses all of Maine, but excludes New York. The study area explicitly incorporates a tier of New York grants in adjacent areas in the Champlain and Hudson valleys, the Taconic Mountains, and on Long Island, and a group of erstwhile Massachusetts towns in what is now western Maine. The roughly rectangular block covers 1.3×10^5 km^2 and ranges from latitude 40°35′ N to 45°40′ N and longitude 69°55′ W to 73°55′ W.

The sample area (Fig. 1) lies across eight physiographic sections and incorporates varied geomorphology from the coastal plain along the Atlantic Ocean to the Appalachian Mountains (regularly to 1200 m a.s.l.) in the north and west (Fenneman, 1938). The topography of New England is mainly a rolling upland surmounted with residual ancient (Precambrian Period) mountains lowering gently towards the sea. The mountains consist of three discrete ranges, each a separate physiographic section. The eroded Taconic Mountain Section is along the New York border, the long-folded Green Mountain Section is in Vermont, and the younger, rugged (maximum 1916 m a.s.l.), intrusive White Mountain Section is in northern New Hampshire extending into adjacent Vermont and Maine. The bedrock geology of New England is commonly a metamorphic complex last uplifted in the Devonian Period and decidedly acidic in reaction. The major exceptions are the carbonate rocks of the Champlain Lowland Section, the Valley of Vermont (part of the Taconics) and, to a lesser extent, the eastern Vermont uplands. The Hudson Valley Section forms a distinct trough connecting with the Champlain Valley through Lake George. The flat Seaboard Lowland Section is a strip bordering the uplands in southern Maine, eastern Massachusetts, Rhode Island and southern Connecticut. Several major south-flowing river valleys (e.g. Hudson, Connecticut, Merrimack, Androscoggin) form low-altitude corridors through the dominant central New England Upland Section. The glaciers left a generally thin layer of stony glacial till over most of the area, except for post-glacial seabed in the Champlain Valley and central Maine lowlands and alluvium in major river valleys. Prominent moraines and outwash are

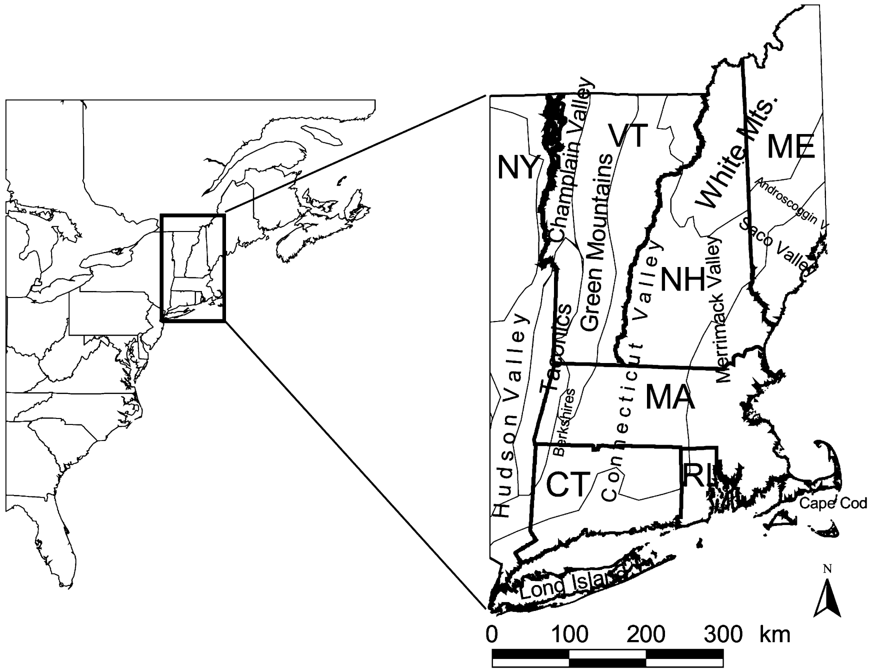

Figure 1 Study area on the east coast of North America and indicating the location of place names cited. State outlines in heavy lines New York (NY), Vermont (VT), New Hampshire (NH), Maine (ME), Massachusetts (MA), Connecticut (CT) and Rhode Island (RI). Outlines of the Physiographic Sections of Fenneman (1938) indicated in light lines.

found on Cape Cod and the Long Island Section. Glacial melt also left sandy outwash plains in some of the lowlands, particularly the Merrimack Valley. The climate varies latitudinally and altitudinally across the region, but all sites have a humid temperate continental climate with an even distribution of roughly 1100 mm annual precipitation with one-fourth as snow in the north (Trewartha, 1968). Mean annual temperatures vary from 5.5 °C in the north to 9.5 °C in the south. Most sites have cool summers, except at the southern edge of the region where summers warm to over 22 °C in July.

Town sample

We searched repositories of town records throughout the study area to locate proprietors' records, field books, manuscripts, maps and published records of town land surveys before settlement. Recorded surveys were regularly found in the Proprietors' Books typically housed with the land records in their respective town clerk's, county registry of deeds, or state/colonial public records offices. Lotting surveys are the primary authority for each town, but when they are lacking or cite a minimal number of trees, they were supplemented with other sources containing equivalent contemporary tree data. In general, all surveys from granting of the town until completion of the lotting of unsettled land, and if necessary, up to 80 years of deeds, were included in the data base. Each 'town' with fifty or more trees was considered to have an adequate sample to estimate town-wide composition (Bourdo, 1956; Whitney & DeCant, 2001). Moreover, in order to obtain a sufficient number of stems, surveys from adjacent towns were occasionally combined to produce a sample for a 'composite town'. All data were taken directly from primary documents or verbatim copies (i.e. transcriptions, microfilms, photocopies, printed records), except for ten town surveys which were already compiled in secondary sources (i.e. Torbert, 1935; Winer, 1955; Hamburg, 1984; Whitney & Davis, 1986; Loeb, 1987; Glitzenstein *et al.*, 1990).

The outlines of the original grants represent the sample units, nominally 'towns'. The boundaries of these 'parent' towns/tracts were derived from historical records, foremost being the initial surveys themselves. Many have changed names or been subsequently subdivided yielding multiple towns as they exist now (Melnyk, 1999). The surveys cover different parts of the original town and in many instances the exact positions of the sample trees were located. Despite this potential spatially explicit control, tallies were simply taken from the town as a whole at a nominal grain size of 100 km^2.

Tree sample

Objective conclusions depend on the tree records being an accurate representation of town vegetation. Land division documents were carefully read for any 'mentions' of trees within each town. All specifically identified witness or boundary trees were tallied by the name given by the surveyor. General listing of the composition of the vegetation or the numerous citations of survey 'posts' or 'stakes', even if identified by species, were excluded from the tally. Because of intermittent citation and difference in structure from trees, all identifiable shrub species were similarity not included in any totals. Thus the sample consisted only of trees actually growing, or dead standing, at predetermined survey points. Throughout proprietary lotting surveys, virtually all tree citations were of a single stem at each corner or end of an outline segment, on a variable (primarily a 20–40 ha) grid. Whenever possible, the sample points were located on an original lotting plat, and a special effort was made to avoid duplication of lots or trees shared between adjacent parcels. Some tallies did contain inadvertent 'multiple counting' of trees, but other than increasing the number this is inconsequential to the relative proportions of taxa from the town. Lotting surveys were not a random sample of the trees and they occurred in widely different patterns and intensities. The uncontrolled survey design produced samples at quasi-regular locations determined *a priori* and drawn from the whole town. These samples are assumed to be proportionally representative of the town-wide composition. As with much historical data, the sampling methods were variable and poorly documented, but there was apparently no consistent bias in the choice of trees, in tree identification, or in their spatial placement (Bourdo, 1956; Siccama, 1963; Grimm, 1984; Whitney, 1994; Russell, 1997; Cogbill, 2000; Whitney & DeCant, 2001). At face value, the lotting tree tallies were a reliable statistical sample and their frequencies were an unbiased estimate of overall forest composition of the towns before settlement.

Common names are used exclusively in this work. The land surveys invariably cited English colloquial names, and many of the surveys were carried out before the introduction of the Linnaean system in 1753. Surveyors were discerning naturalists and remarkably consistent; thus their vernacular usage is accepted (Cogbill, 2000). The surveyors, however, often did not distinguish species within genera and there is additional ambiguity with some unusual or questionably applied names. Thus for reduction in taxonomic uncertainty and consistency across all towns, the named trees are classified into widely represented genera. The categories are strict divisions by genus, except for groups defined by ambiguous surveyor's names. Ironwoods include both *Ostrya* and *Carpinus*. Cedar includes two genera, and as treated here, the present range disjunction separates *Thuja* (northern) from *Chamaecyparis* (Atlantic). 'Whitewood' is not classified as it certainly includes the sympatric *Liriodendron,* sporadically *Tilia* ('basswood'), some *Populus* (in part, now cottonwood), and possibly some *Acer* ('white maple'). Additionally, following the vernacular usage of the time, 'walnut' alone is considered under *Carya* and 'witch hazel' or 'hazel' is treated as *Ostrya* (Cogbill, 2000). All common names are corrected for equivalence in spelling and form and associated with the most exact scientific taxa as compiled in Appendix 1 where nomenclature follows Gleason & Cronquist (1991).

The relative frequency of each taxon across each town is an estimate of the presettlement abundance at that location. Because of the sample size of trees within towns, the precision of the frequency estimates is roughly one tree in 200, i.e. 0.5%. Restricted types or infrequent species were incompletely sampled, but the analyses explicitly focus on an accurate spatial estimate for the common species responsible for gross vegetational patterns. Moreover, scattered towns have samples of thousands of trees and this accounts for some estimates of the range (detection limit of about one tree in 1000, i.e. 0.1%) and the occurrence of uncommon taxa. The lumping of species within some genera necessarily loses resolution in taxa with several common species, such as birches (*Betula*), pines (*Pinus*), ashes (*Fraxinus*), or oaks (*Quercus*). To preserve some of the distinction between species, all separate vernacular names are maintained and their frequency by constancy (number of towns) and occurrence (number of trees) calculated (Appendix 1). Moreover, when congeneric species were specifically distinguished in the same survey, ratios between the numbers of trees in these taxa are used to estimate the local ratios of particular species.

Vegetation analysis

A matrix of proportions of genera within all the sample towns described the basic tree distribution and composition across the study area. Analysis of the vegetation structure and relationship among taxa was further elucidated by a reciprocal ordination of both taxa and towns with detrended correspondence analysis (DCA) using PC-ORD software (MjM Software Design, Gleneden Beach, OR) (McCune & Mefford, 1997). The towns were also classified using a Cluster Analysis (Euclidian distance measure with Ward's Method in PC-ORD). This clustering agglomerated a series of units by minimizing an 'objective' function of the variance among the average composition (centroids) of the groups (Legendre & Legendre, 1998). Both the patterns in the indirect ordination and the hierarchy within the classification allow for identification of the natural groups in the vegetation. The heterogeneity of the unit was calculated as the average Euclidian distance within the group. The vegetational similarity between groups was scaled by the objective distance at which they were joined (i.e. 'fusion distance') within the hierarchy (McCune & Mefford, 1997; Legendre & Legendre, 1998).

Additionally, basic geographical, topographic, and climatic parameters were analysed to determine their association with the vegetation and its divisions. Both Pearson's product–moment (r) and Kendall's rank (τ) correlations and scatter plots of taxa frequencies along the ordination axes and directly against environmental variables (with proportions arcsin transformed for normality) indicated the association of specific taxa with the environment (Sokal & Rohlf, 1981; McCune & Mefford, 1997). Similarly, correlations of environmental variables with the ordination axes indicated the importance of factors underlying the overall vegetation variation. Furthermore, multiple single classification ANOVAs were used to test for the significance and ranking of individual environmental variables in discriminating differences between the classification units (Sokal & Rohlf, 1981). Finally the vegetation composition was summarized by mean proportion of each taxon over all towns falling within defined classes such as state, type, cluster or environmental parameter.

Spatial analysis

In order to elucidate spatial patterns in the vegetation, several data layers in a geographical information system (GIS) were developed for the sample area. ARCVIEW® GIS 3.2a (Environmental Systems Research Institute, Inc., Redlands, CA) enabled analyses of the geographical distribution and relationships among the taxa groups, vegetation clusters and environmental factors across the sample area. The proportions of taxa were simply displayed as individual points positioned at the central geographical (latitude, longitude) coordinates of the sampled town. The spatial pattern of the abundance of individual taxa across the whole study area was also expressed as an integrated surface derived from the network of town samples. The SPATIAL ANALYST extension in ARCVIEW interpolated an abundance surface (0.02 degree grid using inverse squared-distance weighting of the five nearest neighbours) for each taxon. This surface smoothed relative frequency across the entire study area and displayed a continuous (roughly 6 km^2 scale of resolution) distribution preserving the linear combination of proportions in species composition. Several taxa reached their effective geographical limit within the study area. The current composite species ranges of these taxa were mapped for comparison with the presettlement sample. Tree atlases (Little, 1971, 1977) were the basic source for current distributional limits, and the distributions were supplemented using specific local studies (i.e. J. Goodlett & G. Zimmerman, unpubl. obs.; Manning, 1973; White & Cogbill, 1992). The distribution of presettlement vegetation at a regional scale was also compared with various modern classifications, vegetation maps and descriptions of forest types (e.g. Braun, 1950; Westveld *et al*., 1956; Kuchler, 1964; Bailey, 1976; Keys *et al*. 1995).

Environmental analysis

As environmental variables are more properly associated with the entire area of the sampled town, a series of environmental attributes of the town polygons were derived from spatial surfaces created by SPATIAL ANALYST. GIS resampling (mean 168 grid cells) of a USGS (0.01 degree) Digital Elevation Model (DEM) grid produced estimates of town-averaged topographic variables [mean altitude (m a.s.l.), maximum and minimum altitude, and standard deviation (SD) of altitude or 'ruggedness']. As variable local topography averaged out at the town scale, the integrated slope or aspect is a trivial horizontal surface. The potential direct solar radiation flux summed over a midsummer day (27 July) was indicative of the topographic moisture regime and was directly calculated from latitude (Frank & Lee, 1966). Furthermore, the distance in metres from the generalized coniferous/deciduous ecotone in the north-east determined an elevation index combining altitude and latitude [FCE (from conifer ecotone) elevation = Altitude (m a.s.l.) + 100 × Latitude (°) – 5129] (Cogbill & White, 1991).

Several GIS climatic surfaces were also created from a network of 255 climatological stations across the region (data from Climate Atlas of the Contiguous United States, National Climate Data Center, Meteorological Service of Canada). For each climate station on the prevailing land surface (excluding high-altitude stations), a Fourier analysis of the monthly mean temperatures, normalized to a 30-year (primarily 1960–90) period, determined a sinusoidal fit to the annual temperature curve expressed in three coefficients: the mean annual temperature (°C), the amplitude of the annual temperature curve (°C) and the seasonal lag of the curve (*d*) (Cogbill & White, 1991). SPATIAL ANALYST then created an interpolated surface (0.0262 degree grid using inverse squared-distance weighting of the five nearest neighbours) for each Fourier coefficient, as well as surfaces for the daily range of temperature and annual precipitation. All surfaces were resampled for all (mean 24) grid cells within each sample town to derive the mean and extreme values over the entire town. These averaged interpolations intentionally smoothed the variability across the area, but they were directly tied to the local empirical climate regime. They also represented complex climatic patterns, especially in variable terrain, much better than linear regressions (cf. Ollinger *et al*., 1995). Climate also varied with altitude, but the prevailing land surface best represented the average conditions experienced by the vegetation across a town. In addition, the inclusion of independent topographic parameters potentially accounted for altitude variation. The interpolated Fourier coefficients of mean (T_{bar}) and amplitude (T_{amp}) determined the estimated annual temperature curve for each cell or town which was evaluated for mean January temperature ($T_{bar} - T_{amp}$), mean July temperature ($T_{bar} + T_{amp}$), solved for the length of the frost-free growing season [G_{Season} = curve days (d) > 10 °C], or integrated for Growing Degree Days [GDD (°days) = area > 10 °C].

RESULTS

Sample towns

Overall 389 'towns' in the study area had surveys citing at least fifty witness trees (Table 1). Lotting surveys (1623–1850) contained in Proprietors' Records or Maps were the sole source for 79% of the sample (306 towns), while a minority of town compositions were derived from grant outlines or large subdivisions of the town (twenty towns), records in early deeds for the original sale of lots (seventeen towns), surveys of the course of the original roads in town (eight towns), or mixtures of more than one source (thirty-eight towns). The median town size of 119 km^2 is close to the classic 100 km^2 proprietory New England town. The eighteen 'composite towns' are larger than single towns and together with the relatively large older parent towns in southern New England produce a mean 'town' (sample grain) size of 150 km^2. Sample towns are spread across the entire region and are drawn from 45% of the actual land area. Coverage varies from *c*. 75% of the land sampled in southern New England to *c*. 25% of the land covered in the northern regions. The densest sample of towns is from eastern

Table 1 Characteristics of sampled towns and trees included in the New England study area

	State							
	ME	NH	VT	MA	CT and RI	NY	Overall	Range
Dates (AD)	1662–1835	1673–1850	1763–1820	1623–1835	1642–1818	1760–1811	1623–1850	
Towns (number)	21	47	97	118	67	39	389	
Town size mean (km^2)	214	144	117	134	175	207	150	23–1066
Trees tallied (stems)	4473	17,735	23,496	52,403	45,560	10,265	153,932	
Trees per town (median)	112	235	165	200	444	187	200	50–4404
Sample density (trees km^{-2})	1.4	2.9	2.4	3.7	3.8	2.1	2.6	0.09–49.5
Taxa cited per town (mean)	17.5	17.3	16.0	18.5	21.7	18.9	18.2	5–45
Area in sample (%)	26	28	46	76	77	31	45	

Connecticut, north-central Massachusetts and western Vermont, while the sparsest representation is from south-eastern Vermont, eastern New Hampshire and western Maine.

Sample trees

Overall, 153,932 trees were tallied in the study area with a mean of 396 (median 200) trees per town (Table 1). The sample density over the study area averaged 2.6 trees km^{-2}. This represented one tree every 38 ha which, not coincidentally, was nearly the size of a traditional 100 acre (40 ha) farm lot. Also, the sample intensity was only slightly less than the range (2.9–6.7) of sample trees km^{-2} found in public land surveys in other regions of the United States (Schwartz, 1994; Delcourt & Delcourt, 1996).

The early New England lotting surveys recorded 136 separable colloquial names for trees (Appendix 1). An additional sixteen shrub names (most abundant: sassafras, alder, willow and moosewood) were not included, but comprise only 0.3% of all stems. Some thirty-six of the tree names, representing only 214 (0.1%) stems, were odd descriptive combinations, enigmatic vernacular usage, or otherwise unrecognizable even as to genus (Cogbill, 2000). The 100 recognizable names could be combined by synonymy to document at least fifty-one distinct tree species found in these surveys. All these identified species were prominent members of the *c.* sixty-four species in the region's modern tree flora (Little, 1971, 1977). The most commonly used names were 'white oak' with 21% of all citations, followed by 'beech' (12%), 'black oak' (11%), 'hemlock' (7%), 'maple' (6%) and 'pine' (6%). Five genera contain multiple common species which were not distinguished; but, based on the ratio when specifically cited, the most named species in the generic groups were white oak (55% of named oaks), pitch pine (51% of named pines), rock or hard maple (66% of named maples), black birch (49% of named birches), and white ash (48% of named ashes) (Appendix 1).

Despite the lack of species distinctions, generic groups alone clearly express the regional composition. Altogether forty-five of the identifiable species and 99.7% of all the stems can be unequivocally placed into one of twenty-two categories. The uncommon, but still recognizable genera (e.g. apple, mountain ash, red cedar, mulberry) total only 193 stems or *c.* 0.1% of the sample. The number of taxa named in each town varied with the locality and the number of trees cited, but the towns have a mean of 18.2 separately named taxa incorporated into a mean of 10.8 generic groups found in each sample (Table 2). The richness of the tree names is greatest (21.7) in Connecticut towns (where up to 4400 trees were cited in one town) and least (16.0) in Vermont towns (Table 1).

The mean generic composition over the 389 towns is a grand-scale view of the vegetation in New England over 200 years ago (Table 2). Only fourteen genera, which were found in more than 30% of the towns, were regionally prominent. Oaks (*Quercus*), with a mixture of hickories (*Carya*) and chestnut (*Castanea*), were distinctive in the southern states, while beech (*Fagus*) with a mixture of hemlock (*Tsuga*), birch (*Betula*), spruces (*Picea*) and maples (*Acer*), typified the northern states. Among all towns, oaks (30%) and beech (17%) were absolute dominants. Eight other major taxa had much lower mean town proportions from 9 to 2.5% in descending order: pines, maples, hemlock, spruces, birches, hickories, chestnut and ashes. Together the ten most common genera also comprise 95% of the tree citations and all, except chestnut, were widespread, occurring in more than 60% of the towns. Interestingly, 50.1% of the tree abundance in the region, including the top two and the ninth ranked genera, are from a single plant family (Fagaceae). All genera beyond the twenty-two categories, except the composite 'whitewood', were found in less than twenty towns (5%). Despite being distinctive elements in the flora, other genera and their constituent species, were evidently inconsequential to the prevailing composition of the forest.

Oaks, beech, pines and spruces clearly dominated the vegetation in some towns, with $> 50\%$ maximum abundance. Although of moderate abundance, maples and birches were nearly ubiquitous, found in more than 90% of the towns. Additionally each of the common taxa (except for ash), plus fir (*Abies*), could be locally important, with $> 20\%$ maximum abundance in individual towns. A series of secondary genera [i.e. elms (*Ulmus*), ironwoods (*Ostrya* and *Carpinus*), basswood (*Tilia*), poplars (*Populus*), butternut (*Juglans*), cherries (*Prunus*)] were regularly (23–60% constancy) found in scattered towns, and despite having low ($< 1\%$) overall representation, reached moderate (3–10% maximum) local abundance. Three conifer genera [fir,

Table 2 Average town-wide presettlement generic composition (relative frequency*) within New England states and among all sample towns

	ME	NH	VT	MA	CT and RI	NY		All Towns		
Towns	21	47	97	118	67	39	All trees	389	389	389
Sample stems	4473	17,735	23,496	52,403	45,560	10,265	153,932	Mean	Maximum	Constancy†
Taxa	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
Oaks	16.1	11.8	2.1	45.4	59.5	33.7	39.5	30.2	82.1	80.2
Beech	10.6	25.5	36.0	6.1	3.0	15.7	12.1	16.6	68.2	75.6
Pines	14.6	12.3	2.2	15.9	3.1	8.5	9.6	9.0	69.8	75.3
Maples	10.7	9.4	15.3	6.4	4.1	7.8	7.7	9.0	30.8	94.9
Hemlock	8.7	14.7	11.1	6.3	2.6	9.8	6.7	8.4	39.6	74.3
Spruces	13.7	10.0	12.3	1.2	0.4	3.0	3.1	5.7	52.6	62.5
Birches	12.3	8.2	8.6	3.2	2.5	3.7	4.2	5.6	37.8	91.8
Hickories	0.2	0.3	0.2	4.5	9.8	4.3	5.2	3.6	23.7	59.9
Chestnut	0.0	0.8	0.1	4.5	8.6	3.7	4.4	3.3	31.7	46.5
Ashes	2.7	2.2	2.6	2.4	2.8	2.5	2.6	2.5	11.7	84.1
Fir	5.2	1.5	2.5	0.0	0.0	0.1	0.4	1.1	24.2	22.9
Elms	0.5	0.7	1.4	0.8	0.6	1.3	0.9	1.0	8.2	59.6
Basswood	0.4	0.9	1.9	0.4	0.3	1.2	0.7	0.9	7.6	49.9
Ironwoods	0.4	0.3	2.0	0.4	0.4	1.3	0.8	0.9	9.5	50.1
Poplars	2.0	0.9	0.2	1.2	0.9	0.8	0.9	0.9	10.0	55.5
Cedar (northern)	1.5	0.1	0.7			0.4	0.1	0.3	7.1	13.4
Butternut	0.0	0.1	0.3	0.1	0.3	0.4	0.2	0.2	8.6	22.6
Cherries	0.1	0.1	0.2	0.2	0.2	0.3	0.1	0.2	3.8	27.5
Cedar (Atlantic)	0.0	0.0		0.4	0.1	0.2	0.2	0.2	6.6	13.4
Pepperidge	0.0			0.0	0.2	0.3	0.1	0.1	5.5	8.7
Tamarack	0.2	0.1	0.1	0.0	0.0	0.2	0.0	0.1	5.7	5.1
Buttonwood	0.0	0.0	0.0	0.1	0.1	0.0	0.1	0.1	2.2	11.1
Other	0.4	0.1	0.1	0.5	0.6	0.7	0.3	0.4	–	–

*A 0.0 indicates trace (< 0.05%), while no entry indicates not recorded.
†Frequency of towns in which recorded.

northern cedar (*Thuja*), tamarack (*Larix*)] had low overall abundance, but could be important (> 5%) in the north. In the south, Atlantic cedar (*Chamaecyparis*) and pepperidge (*Nyssa*) had scattered low abundances.

Presettlement composition

The amalgamation of genera forming the presettlement vegetation of New England is dramatically displayed as pie charts of taxa proportions arrayed within the sampled towns (Fig. 2). Despite expected local variation, there was a strong spatial correlation in the compositions among towns. Pronounced geographical patterns were evident as the northern conifer species (greens: spruces, fir, cedar, tamarack) blended through 'northern hardwoods' (reds: beech, birches, maples) to 'central hardwoods' (yellows: oaks, chestnut, hickories) in the south. The temperate conifers (blues: pines, hemlock) fell roughly between the two hardwood sectors, with pines mixing to the south and hemlocks to the north. Although all towns had a decidedly mixed assemblage, four genera consistently characterized distinct geographical regions. The transition from spruce through beech to pine and then to oak prominence roughly paralleled the physiographic change from northern mountains through the uplands to the southern lowlands. Within this gross gradient, locally distinctive patterns, generally a more equitable mix of genera, appeared in the transitions, especially between the oak and beech sectors of the Champlain Valley, Taconics, southern Berkshires, north-central Massachusetts and west-central Maine. Major river valleys (i.e. Hudson, Connecticut, Merrimack) displayed a northward extension of oak and pine, while the uplands (western Massachusetts, south-western New Hampshire) displayed complementary tongues of beech and hemlock to the south.

Species distributions

The vegetation pattern was a composite of the individual genera, but each genus had a distinctive distribution and contributed differently to the overall pattern. Maps of interpolated grids of each of the twenty-two taxa displayed continuous surfaces of town-wide frequency across the study area. In addition to range limits, these distribution maps indicated the actual spatial pattern of the taxon's abundance across the range. The dense network of towns and their local consistency in composition resulted in a detailed, and remarkably simple, 'topographic' pattern of isowits. The explicit minimum resolution of these maps was the town scale (c.100 km^2) and areas with fewer towns had more generalized patterns. For the eight common genera that had clear geographical patterns, these abundance surfaces were shown divided into classes of relative frequency beginning at

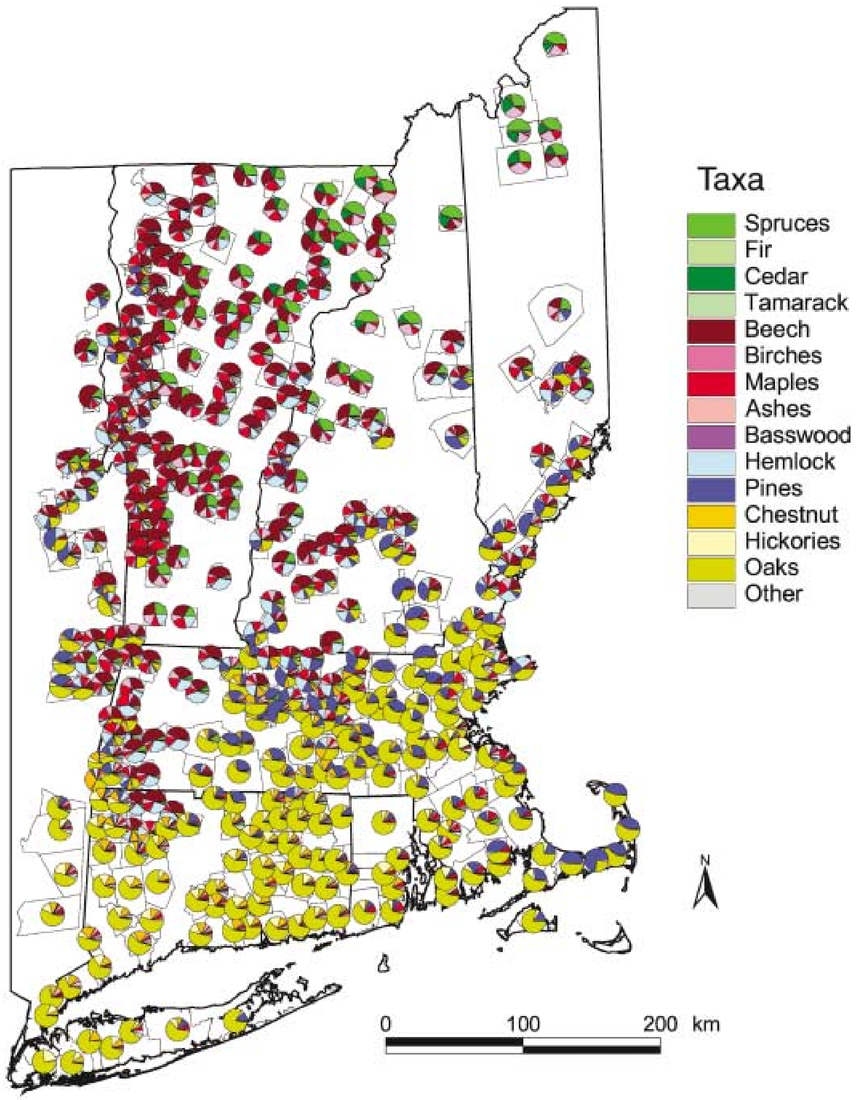

Figure 2 Spatial distribution of the proportions of genera in presettlement surveys arrayed on sample towns. Sample towns outlines indicated in light lines.

the general detection limit of 0.1% (Fig. 3). Individual towns with local extreme values appear as small 'dots' while more regional variability results in 'dappling' on the maps.

Four of the taxa, including the classic 'northern hardwoods' and their common associate hemlock had a distribution centred on the uplands. Beech (Fig. 3a) was the most abundant species throughout most of the uplands and reached its general maximum abundance in Vermont (> 50%). Beech and hemlock shared the dramatic boundary near the southern edge of the uplands and both, despite being within their ranges, fell below the detection limit in southern New England. Beech reappeared as a minor component near the coast. Hemlock (Fig. 3f) had a moderate, but variable abundance on the uplands, with minima (< 10%) in the Green Mountains and Taconics and a maximum presence in western Massachusetts (> 30%). Maple (Fig. 3b), the vast majority 'hard' or 'rock' maple, had the most widespread and equitable distribution of the common genera with a broad maximum (> 20%) centred on north-eastern Vermont and falling to < 5% in the southern lowlands. Birch (not shown) was the least abundant of the northern hardwoods and had a long ridge of maximum abundance in the mountains, varying from > 25% in north-western Maine and gradually decreasing through Vermont to a consistent 10% in the Taconics. Birch consisted of three species which presumably replaced each other as predominant across the genera's wide range. Black birch was clearly responsible for the greater 3% abundance in lowland New England, yellow birch accounted for most presence (> 10%) in the uplands, while white birch mixed with yellow birch combined for the maxima (> 25%) at higher elevations of the northern mountains.

Four conifers had restricted ranges in the northern edge of the study area. Spruce (Fig. 3e) dominated (> 40%) the northern White Mountain region. It was consistently mixed in tongues down the Green Mountains of Vermont (> 20%) and to a lesser extent into south-western New Hampshire (> 10%), and fell to low levels (< 5%) before reaching the

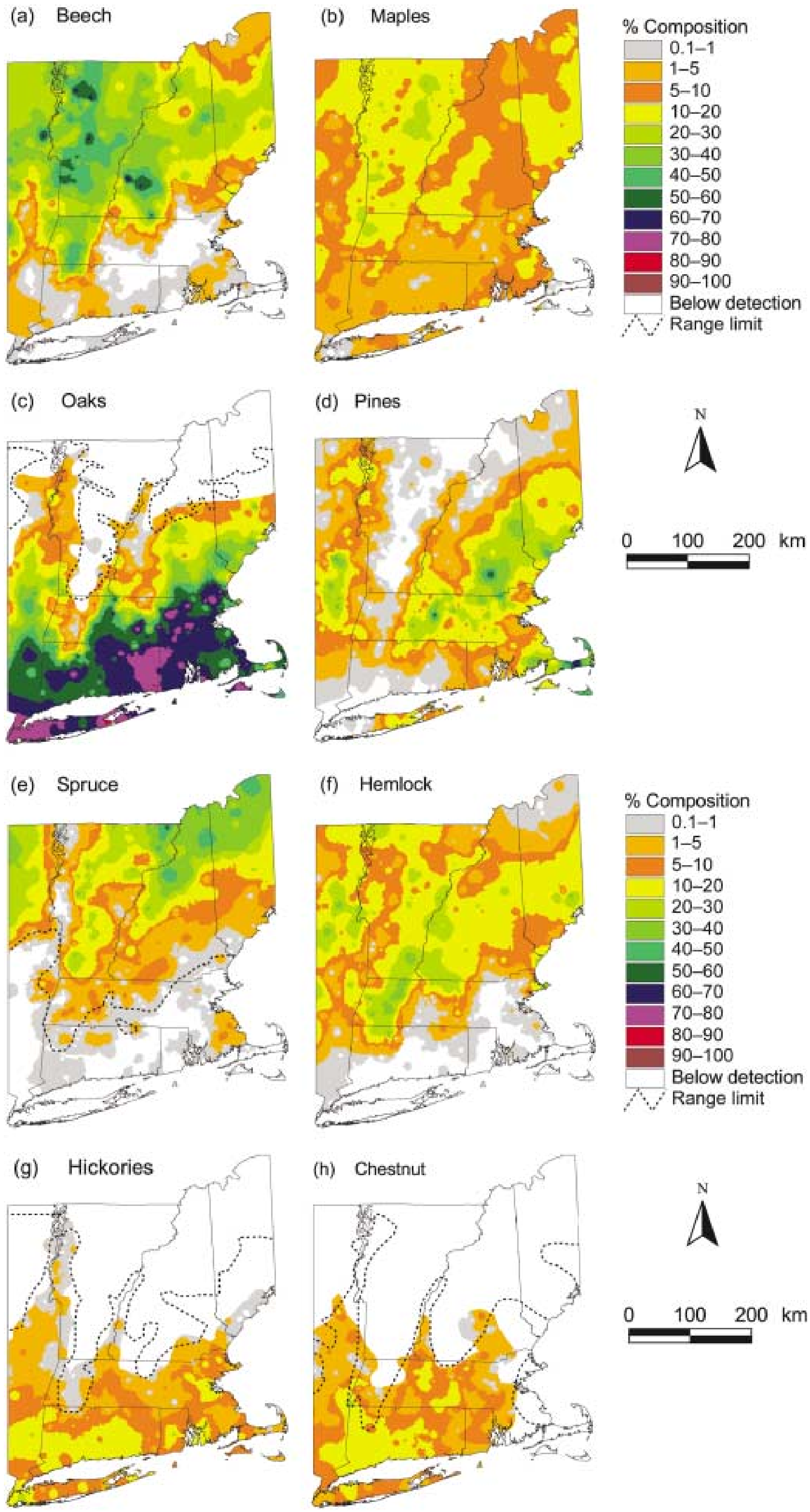

Figure 3 Maps of abundance surfaces of taxa: (a) beech, (b) maples, (c) oaks, and (d) pines, (e) spruces, (f) hemlock, (g) hickories and (h) chestnut in presettlement New England. The interpolated surfaces are shown divided into classes of relative frequency, from the general detection limit of 0.1%. The explicit minimum resolution is the town-scale (*c*.100 km^2). Modern composite species range distribution of (c) oaks from J. Goodlett & G. Zimmerman, unpubl. obs. and Little (1971), (e) red spruce from White & Cogbill (1992), (g) hickories from Manning (1973) and Little (1971), and (h) chestnut from Little (1977) are shown by dashed lines.

edge of the upland. A distinct corridor of low spruce abundance followed the Champlain Valley. The range limit of red spruce closely followed the 1% isowit, but there were significant occurrences of spruce, presumably black, in southern Connecticut and south-eastern Massachusetts. Fir, northern cedar and tamarack were much more restricted than spruce and were locally common only in the northern mountains with rather modest maxima (8–20%) in conjunction with spruce. Interestingly northern cedar also had a secondary maximum (3%) in the southern Champlain Valley, exactly where spruce was below detection.

Three 'central hardwood' (Leopold *et al.*, 1998) genera had ranges restricted to southern New England. Oak (Fig. 3c) had tongues up the Hudson–Champlain, the Connecticut, and a broad extent in the Merrimack Valleys. Oak reached a consistent and remarkably high (> 70%) abundance from Long Island through eastern Connecticut into eastern Massachusetts. Many oak species contributed to this pattern, but the absolute dominant was clearly white oak with more than 67% of the citations in the heart of the oak forest in eastern Connecticut. Notable amounts of white oak also extended to the slopes of the White Mountains and into the Champlain Valley. The commonly combined pair, black and red oaks, were regular associates with white oak in many southern areas and red oak formed the range limit on the northern uplands. Despite being below the detection limit in the small range extensions into northern valleys and central Maine, oak's presettlement range closely traces its current range. Within its range, oak had low abundance (< 5%) in the uplands in western Massachusetts and south-western New Hampshire, but is more important (> 20%) just to the south in the Taconics. Hickory (Fig. 3g) has a modern range which is similar to, but more restricted than oak and is virtually missing from New Hampshire. Its presettlement range actually followed the current range (a combination of shagbark and bitternut) fairly well, except for falling below detection in central Maine and the upper Connecticut Valley. Interestingly, hickories reached or exceeded the putative modern range in the Champlain Valley. Despite paralleling the oak range, hickories had much lower abundances and reached maxima (15%) both well to the west of oak in Connecticut and in spots in the eastern edge of oak's dominance in eastern Massachusetts. Hickories also barely penetrated the uplands and were in very low abundance in western Massachusetts. Chestnut (Fig. 3h) followed the hickories range very closely, but was missing from the immediate coast to the east. It was also below the limit of detection within its modern range in the Champlain Valley and in Maine. Chestnut has been much altered in abundance because of blight (Paillet, 2002), but had its prominent maxima (> 10%) in western Connecticut as did hickories, but differed in having a marked second maxima in central Massachusetts. Although possibly poorly documented today, chestnut was found beyond the mapped range in much of western Massachusetts and to a lesser extent in the Merrimack Valley. Curiously, chestnut displayed its maximum abundance in a town in the southwest corner of Massachusetts which is on the border of its ostensible range.

Pines (Fig. 3d) had a dramatic distribution with large extended patches pinching either side of central New England. The 10% isowit bounded roughly three polygons: the Hudson–Champlain corridor; an extensive band from central Massachusetts through southern Maine and Cape Cod. The nested maxima of high pine abundance were scattered in pockets in the Champlain (to 20% abundance with 90% of the named trees white pine), Hudson (to 30% with > 75% pitch pine), Connecticut (to 40% with 60% pitch pine), Merrimack (maxima > 50% with 67% pitch pine) and Saco (to 20% with 55% white pine) Valleys. In areas of maximum pine representation in the large southern valleys and on Cape Cod (> 50% pine, almost 100% pitch), pitch pine was clearly predominant. The proportion of white pine increased towards the northern valleys, in concert with a dramatic decrease in overall pine expression. Even on the uplands, white pine increased from *c.* 55% of the named pines in central Massachusetts to nearly all of the citations on the northern uplands, except the Taconics. Although within its overall range, white pine was remarkably uncommon (< 1%) on the New England uplands (Abrams, 2001). Furthermore, any pine species was uncommon or undetectable in a band slicing through Vermont, western Massachusetts, and spreading along the Connecticut coast.

Several other commonly cited genera had distributions independent of the pattern of major species. A series of common hardwood genera reached their modest maxima (< 5%) scattered throughout central New England. Ash, basswood, elm, butternut and ironwood taxa all had patchy but still widespread distributions (Table 2). All also had a joint prominent low peak in the Champlain Valley. Interestingly, each also had various secondary areas of relatively high abundance: both basswood and ironwoods in the upper Connecticut Valley, the Taconics and adjacent New York; ash in north-central Massachusetts and north-western Connecticut; elms in coastal New Hampshire and Massachusetts; and butternut in the Green Mountains and western Connecticut. Poplars had a southern distribution similar to pine, but were below detection in the mountains. Poplars maxima (> 2%) were scattered in central regions from north-central Connecticut to south-western Maine. Cherries had low importance (< 3%) and are scattered throughout the region. Buttonwood reached a maximum in Rhode Island. Two restricted (< 13% constancy) southern species just reached New England and were more common in 'swamps' reaching moderate maxima (7%) in scattered lowland towns. Atlantic cedar was tightly restricted to the southeast coastal area, reaching maxima (> 2%) in south-eastern Massachusetts and Long Island. Pepperidge was rare in Massachusetts, but was relatively more abundant (> 0.5%) in eastern Connecticut and especially (> 1%) on Long Island.

Town classification

The visual overview of vegetation (Fig. 2), together with the patterns of individual genera (Fig. 3), were reiterated by a formal classification of the overall vegetation composition of the 389 towns. The final steps in the Cluster Analysis defined eight separate clusters that correspond well, in number and spatial consistency, to perceived vegetation defined units (Table 3). Three levels of the hierarchy produced objectively derived units at various orders (notably two, four and eight groupings). The dendrogram (Fig. 4) shows the nested rela-

Table 3 Average town-wide presettlement generic composition (relative frequency*) of classification clusters in New England

	Cluster							
	1	2	3	4	5	6	7	8
Towns	14	49	55	62	48	25	91	45
Trees	1441	11,230	17,004	17,603	21,149	11,753	50,022	23,730
Taxa	(%)	(%)	(%)	(%)	(%)	(%)	(%)	(%)
Cedar (northern)	2.6	0.6	0.3	0.4	0.1			
Fir	15.6	3.2	0.6	0.3	0.1	0.0		
Tamarack	0.5	0.1	0.0	0.1	0.1		0.0	
Spruces	39.4	22.1	3.6	3.8	1.7	1.1	0.5	0.1
Birches	21.9	10.6	6.4	6.6	5.9	1.6	2.2	1.2
Beech	8.7	33.9	45.5	26.5	7.9	2.4	0.8	0.3
Hemlock	2.6	11.8	12.0	21.5	10.4	1.9	0.9	0.4
Basswood	0.1	0.7	2.4	1.7	0.6	0.3	0.3	0.1
Ironwoods	0.0	0.7	1.9	2.0	0.6	0.4	0.3	0.2
Maples	7.0	12.6	16.0	14.1	8.6	4.9	4.1	2.4
Ashes	0.7	1.4	2.8	4.0	3.5	1.8	2.4	1.5
Poplars	0.1	0.2	0.4	0.8	1.7	1.1	1.1	0.9
Pines	0.4	0.9	2.2	7.5	19.1	37.9	8.1	6.2
Elms		0.6	1.7	1.3	1.1	0.7	0.8	0.6
Butternut		0.2	0.4	0.2	0.4	0.1	0.2	0.0
Cherries		0.2	0.1	0.2	0.3	0.1	0.2	0.1
Buttonwood		0.0	0.1	0.0	0.1	0.0	0.1	0.1
Oaks		0.3	2.7	6.8	30.5	41.5	58.9	73.5
Chestnut			0.4	1.5	5.3	1.3	7.9	3.9
Hickories			0.3	0.5	1.8	2.1	9.8	7.1
Cedar (Atlantic)			0.0		0.1	0.3	0.4	0.3
Pepperidge					0.0		0.1	0.2

*A 0.0 indicates trace (< 0.05%), while no entry indicates not recorded.

tionships of the cluster groups to one another. For example, clusters 7 and 8 were combined at the lowest order [fusion distance (FD) of 10], while the most distinctive single cluster (cluster 1) remained uncombined the longest. The highest division (last combination FD = 63) separated the eight objective clusters into two primary four cluster groups. In turn, a prominent secondary division (FD = 24) split the southern group into two pairs: clusters 7, 8 (yellows) and clusters 5, 6 (blues). The four northern clusters were closely allied, but a secondary division (FD = 17) divided a mountain cluster (cluster 1, green) from an upland group (clusters 2–4, red). The three upland clusters formed a triplet series with a nearly equal tertiary separation (FD = 13–14). The two southern 'parallel' pairs of clusters were each distinguished at a slightly lower tertiary level (FD = 10–11), and consisted of both the most variable [cluster 5: mean Euclidean distance (ED) = 0.27] and the most homogenous (cluster 8: ED = 0.12) single clusters. By the tertiary level of division in the cluster classification (Fig. 4), the clusters became relatively homogenous, but membership of particular towns within the units became fuzzy (Brown, 1998). Moreover, vegetational unity and geographical coherence weaken with more than eight clusters.

The composite composition (centroid) of the fourteen to ninety-one towns in each cluster demonstrated the slowly shifting importance of specific genera in typifying these units (Table 3). The overriding division was between upland 'northern hardwood' beech, clusters 1–4 and southern lowland 'central hardwood' oak, clusters 5–8. Altogether secondary clustering produced three distinct forest types typified by dominant genus (> 26% mean): spruce (cluster 1), beech (clusters 2–4), or oak (clusters 5–8). At this same level of distinction, the oak cluster was split into a high oak pair (clusters 5, 6) and a transitional pair (clusters 7, 8) with high pine abundance.

The four northern clusters formed a loose concentric pattern in relation to the mountains and were further distinguished by the amount of beech (Fig. 4; Table 3). The spruce cluster 1, was composed of the high conifer towns with the least beech. This mountain cluster had > 50% combined spruce and fir composition with a mixture (*c*. 35%, primarily birch) of northern hardwoods. Cluster 3 formed the nucleus of the northern hardwood triplet with composition totally dominated by beech (46%). A tight 'chain' was formed, first linking with the moderate spruce (22%) cluster 2, then the higher hemlock (21%) cluster 4, and finally with the most distinctive cluster 1. Cluster 2 was found throughout the lower mountains and higher hill towns, cluster 3 was prominent on the lower hills around the perimeter of the mountains, while cluster 4 generally lay in valleys still within the uplands or beyond in the northern lowlands (Fig. 4). Thus the resultant classic northern hardwood unit (clusters 2–4, red) covered much of northern New England and had both a mixed spruce component from the higher elevations and an equitable mixture of hardwood species, including some oak and pine from the lowlands.

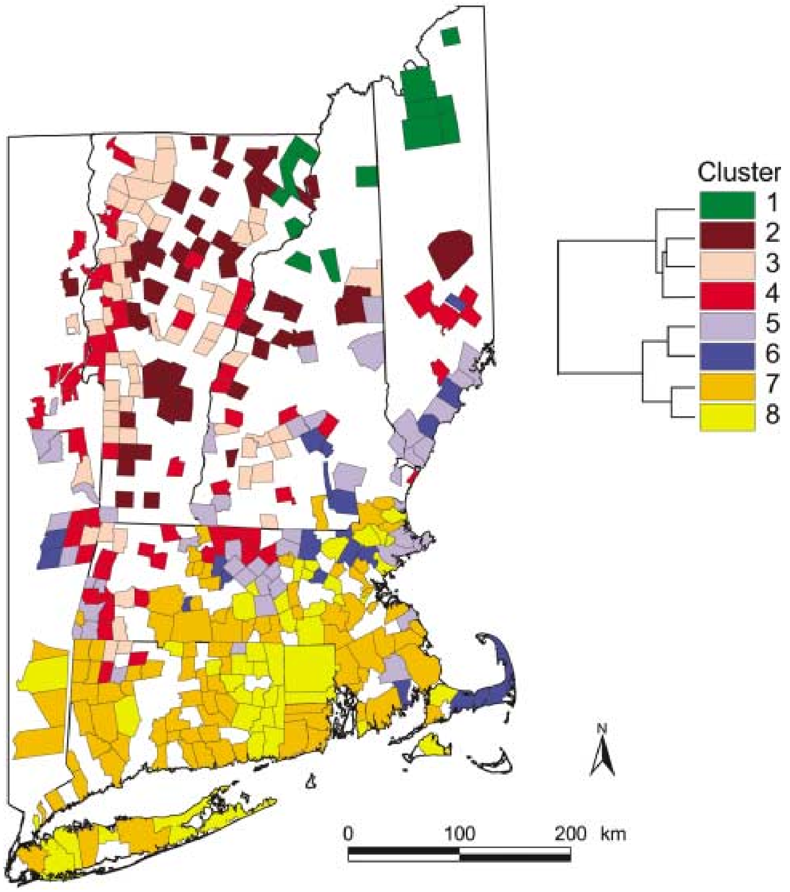

Figure 4 Geographical distribution of towns as classified by Cluster Analysis into eight clusters. The dendrogram next to the legend is scaled proportional to objective distance at which the cluster units are joined (i.e. 'fusion distance') in the hierarchy.

Except for the secondary separation of northern 'transition' oak-pine, the four oak vegetation clusters had weak spatial coherence (Fig. 4). The oak 'transition' (clusters 5, 6) of central regions had a higher component of pine (> 15%) than the typical oak forest (clusters 7, 8) of southern New England (Table 3). The two oak pairs were further separated by major compositional differences in oak. The southern 'typical' oak pair was first split into cluster 8 of very high (73%) oak composition and cluster 7 with less oak (59%) and more balanced composition, including more chestnut. The 'transitional' oak-pine was a combination of a small scattered cluster 6 of high pine (38%) and cluster 5 with low oak (31%). The latter cluster was still typified by oak-pine, but had a distinct mixture of both northern (maples, hemlock) and other southern elements (chestnut).

Ordination

The variation among town compositions was further illustrated by an indirect ordination (DCA) of the towns and genera. The compositional matrix was reduced in dimension so that the 389 towns and twenty-two genera were located along two axes in relation to their similarity (Fig. 5). The constellation of sites showed two clouds along the first axis; the northern sites form a continuous series (from clusters 1–4) to the right side, while the southern oaks (clusters 7, 8) formed a tight aggregation at the other pole. Significantly the variable transitional oak, cluster 5, lay in the thin area just left of centre and the two primary groups could be cleanly separated (clear gap between cluster 4 and cluster 5). The second axis separated the distinct pine dominance (cluster 6) at one end from the secondary southern hardwood genera (chestnut, pepperidge, hickories) drawing some of cluster 7 to the lower pole. In the centre of the space the second axis was muted, but the 'richer' genera (e.g. butternut, ironwood, ash, basswood, elm) drew elements of cluster 4 downward while hemlock was above the axis with other towns of cluster 4, which had a significant mix of hemlock within the hardwood forest. Thus, the ordination confirmed the overall integrity and distinctiveness of the individual clusters, as well as the primacy of the division between the northern and the central hardwoods. At the same time there was obvious variability within the clusters with significant compositional overlap between most adjacent clusters (e.g. clusters 7, 8 and clusters 2–4). The vegetation apparently formed a continuous gradient, particularly in the north (right on ordination), with a change from spruce and fir through beech, hemlock and maple composition. The oak clusters deviated from this gradient and had a more variable composition, especially near the transition.

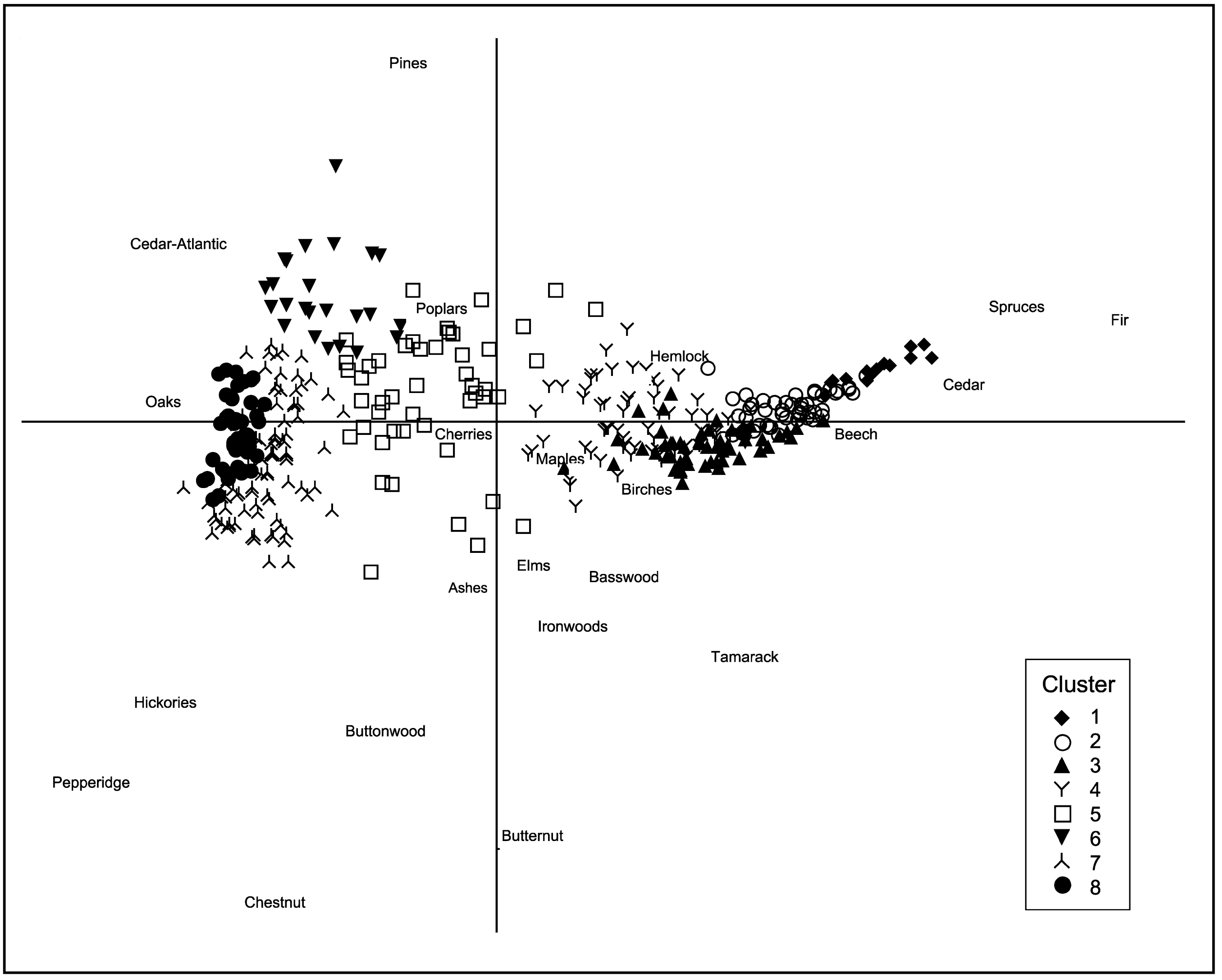

Figure 5 Detrended correspondence analysis ordination of twenty-two genera and 389 towns in the presettlement surveys of New England. Towns are classified by their cluster identity and the genus groupings are labelled at their centroid.

Environmental correlates

The classification and ordination of the presettlement vegetation were driven by compositional patterns, but the underlying relationship to environmental factors was undeniably strong. Each town was characterized by three geographical, five topographic and nine climatic parameters. Their overall statistical summary was a composite of the environment of the study area (Table 4). As ANOVAs for all variables indicated high statistical significance ($P < 0.001$, $F > 3.47$), the town clusters differ markedly from one another on the basis of any of the environmental parameters. There is a tight cocorrelation between most of these environmental variables (average $r^2 = 0.36$ and 0.71 among the climatic variables), so many of the associations are redundant (Table 4). The best discriminator by far, based on ranked ANOVA *F*-values ($F = 237$), was the FCE-elevation (a composite topographic-geographical variable closely correlated with temperature regime) followed by three other allied climate variables, headed by mean annual temperature ($F = 168$). The highest ranked variables of other types [i.e. solar (geographical) and maximum altitude (topographic)] were mixed in with a host of highly significant, but less discriminating ($F < 125$) parameters. The mean environmental parameters of the towns formed a smooth environmental series southward past the vegetation transition into oak. The difference between cluster means (Table 4) indicated the maximum statistical separation was between the spruce (cluster 1) and the northern hardwoods (cluster 2), and secondarily between the upland (cluster 4) and the lowland series (cluster 5). Although still significantly different [$P \leqslant 0.01$, determined by ANOVA least significant differences (LSD)], the oak transition environment (cluster 5) was marginally closer to the northern sites than the neighbouring southern oak cluster (cluster 7). Significantly, there were no statistical environmental differences ($P \geqslant 0.01$) between the two southern oak (clusters 7, 8) clusters. This mirrored the ordination (Fig. 5) diagram where there was a continuous

Table 4 Characteristics of environmental variables across 389 New England towns and individual clusters

	All towns				Cluster									
					1	2	3	4	5	6	7	8		
$n =$	389	389	389	389	14	49	55	62	48	25	91	45	LSD*	F†
Parameter	Mean	Min.	Max.	SD	Mean	Mean	Mean	Mean	Mean	Mean	Mean	Mean	$n_0 = 47.2$	d.f. = [7,381]
FCE-Elevation‡ (m)	−610	−1044	41	244	−98	−265	−442	−543	−676	−781	−823	−842	57	237
Tbar§ (°C)	7.8	3.3	12.2	1.6	4.3	5.9	6.8	7.3	8.0	8.6	9.4	9.4	0.4	168
GSeason** (days)	164	128	203	14	136	148	155	159	165	171	177	177	4	157
Jan. Temperature (°C)	−5.6	−11.4	−0.2	2.3	−10.3	−8.2	−7.2	−6.6	−5.3	−4.3	−3.4	−3.3	0.6	155
GDD†† (°days)	2230	1286	3294	334	1513	1821	2048	2156	2234	2366	2535	2527	97	130
Solar‡‡ (Ly)	966	959	970	2	961	963	964	965	966	967	968	968	1	123
Latitude (°N)	42.9	40.7	45.6	1.1	44.9	44.0	43.7	43.3	42.8	42.6	41.9	41.9	0.3	122
July Temperature (°C)	21.2	18.0	24.5	1.1	18.8	19.9	20.7	21.1	21.2	21.5	22.1	22.0	0.3	94
Altitude max. (m a.s.l)	415	29	1351	298	890	844	586	441	327	162	224	179	97	93
Altitude mean (m a.s.l)	229	8	709	170	542	460	317	255	172	91	120	98	56	89
Tamp§§ (°C)	13.4	10.8	15.0	0.8	14.6	14.0	14.0	13.8	13.2	12.9	12.7	12.6	0.3	75
Altitude min. (m a.s.l)	118	0	457	108	360	236	167	129	97	45	49	42	39	67
Ruggedness*** (m)	66	6	248	49	112	133	90	70	51	27	42	31	19	51
Precipitation (mm)	1091	843	1317	101	1016	1031	1015	1035	1115	1094	1169	1170	41	39
Seasonal lag (days)	30.6	28.3	38.5	1.5	30.3	29.8	29.7	29.9	30.6	31.9	31.3	31.6	0.7	22
Longitude (°W)	72.2	73.8	70.0	0.9	71.2	72.4	72.8	72.7	72.0	71.3	72.3	71.9	0.4	15
Daily Range (°C)	11.8	7.6	14.1	1.2	12.3	11.8	11.6	12.1	12.2	11.4	11.6	11.4	0.6	4

*Least significant difference between group means at $P = 0.01$, $\mathrm{LSD} = 2.58 \times \sqrt{(2 \times n^{-1} \times \mathrm{MS}_{within})}$.
†ANOVA variance ratio, for $P = 0.001$, $F_{[7,381]} = 3.47$.
‡Elevation from the coniferous ecotone.
§Mean annual temperature.
**Growing season length > 10 °C.
††Growing degree days > 10 °C.
‡‡Potential direct beam flux summed for 27 July (in Langleys day^{-1}; 1 Ly = 4.18 J cm^{-2}).
§§Amplitude of the annual temperature curve.
***SD of altitude.

gradient on the first axis until the three southern clusters were reached. The clusters then spread on the second axis.

The trends in environmental significance were formalized by the correlation analysis of the same variables in the ordination. All environmental vectors, except longitude, projected into the ordination space (not shown) were rotated only a few degrees counterclockwise (FCE-elevation was virtually coincident) from the first ordination axis. The highest correlation with the first ordination axis was with FCE-elevation ($r^2 = 0.82$, $\tau = -0.73$) followed by mean temperature ($r^2 = 0.76$, $\tau = -0.69$) and several similar climatic variables, with latitude the best geographical correlate ($r^2 = 0.71$, $\tau = 0.64$). Interestingly, the second ordination axis had low significance against most environmental variables ($r^2 < 0.04$), but a high correlation with longitude ($r^2 = 0.29$, $\tau = 0.37$), primarily reflecting the strong tendency of the high pine clusters to be on the east side of the area.

The responses of genera to the environment were quantified by direct gradient analysis of the composition (coenocline) along the environmental axes (Whittaker, 1975). All genera except ash, cherry, elm and butternut had statistically significant (generally $0.25 < r^2 < 0.60$) correlations with the suite of environmental variables. Depending on the taxa, the highest correlations were found in either FCE-elevation, mean annual temperature, January temperature, or latitude. The average town generic composition within FCE-elevation classes displayed the broadly overlapping ranges of the common species (Fig. 6). The dominance of oaks below 600 m FCE-elevation and the dominance of beech to just (150 m FCE-elevation) below the actual coniferous ecotone where it was exceeded by spruce is clearly demonstrated. Similar plots against latitude (Fig. 7) had exactly the same pattern with crossover at 43.0°N and 45.0°N. While three major 'zones' were evident both latitudinally and elevationally, variation was subsumed in the mean values, and the clusters of specific composition were obscured. The response of the three dominant species to mean annual temperature (Fig. 8) showed the same statistically significant responses (oak $r^2 = 0.69$, spruce $r^2 = 0.48$, and beech $r^2 = 0.37$, lower as a result of normal distribution). The average curves still crossed (at 7.3 and 4.5 °C), but the details, such as large variance in all species and patches of low abundance (e.g. 'warm' spruce) began to appear. Most dramatic was the consistency of oak in the warm sector and its decline below 8 °C.

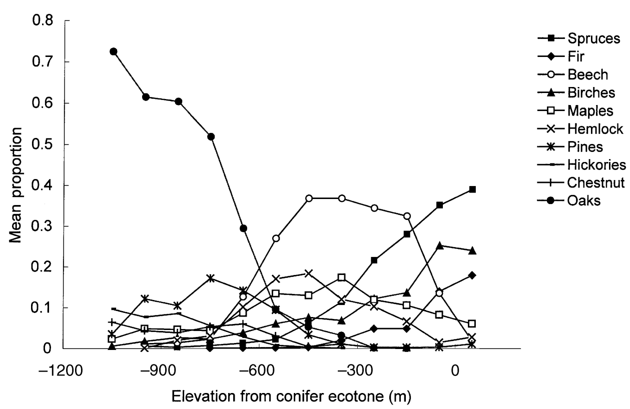

Figure 6 Coenocline plot of town average presettlement composition by classes of FCE-elevation (distance from the conifer ecotone). Mean of town-wide relative frequencies are plotted at the midpoint of 100-m classes.

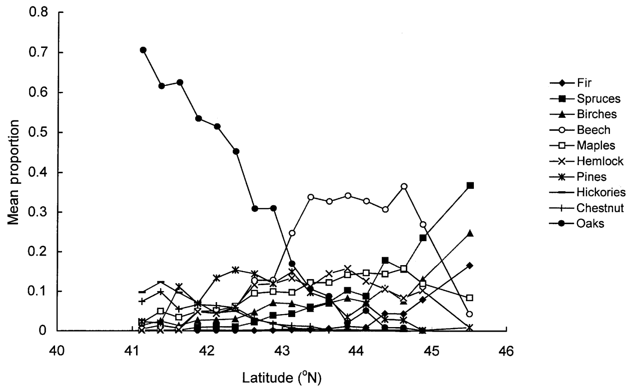

Figure 7 Coenocline plot of town average presettlement composition against classes of latitude. Mean of town-wide relative frequencies are plotted at the midpoint of 0.25 degree classes.

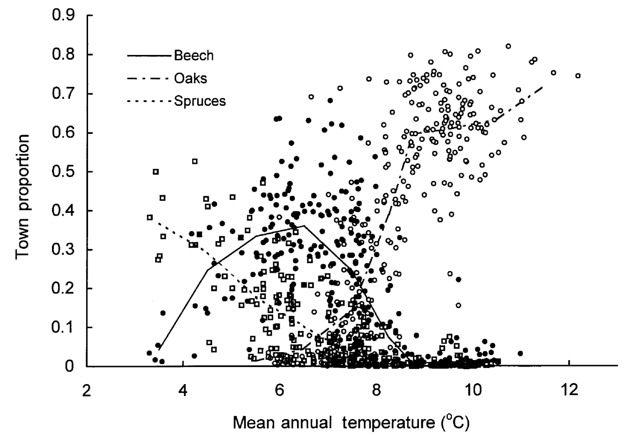

Figure 8 Plot of town-wide (open circle) oak, (solid circle) beech, and (open square) spruce presettlement abundances against mean annual temperature. Lines connect means in 0.5 °C classes plotted at the midpoint.

DISCUSSION

New England tension zone

The geographical, vegetational and environmental patterns all demonstrate a broad regional gradient among towns across New England and reiterate the gross latitudinal trend in the vegetation. Embedded in this trend, however, is a distinct division separating 'northern' and 'southern' vegetation (Figs 2, 4 and 5). This discontinuity reflects the coincident boundary of a suite of taxa abundances (i.e. especially beech, hemlock, oaks, hickories, chestnut, and to a lesser degree spruce and maples). The boundaries are relatively abrupt, and interestingly in several cases, are not actual range limits (Fig. 3). This steepening of the vegetation gradient most simply marks the shift from oak to beech dominance and indicates the presence of a vegetation ecotone. An objective linear approximation of the position of this discontinuity was constructed by following the joint boundary (or splitting the gap between town outlines) of the towns constituting cluster 4 (rarely cluster 2 or 3) with those in cluster 5 or 7 (rarely cluster 6) (Figs 4 and 9). Only seven towns were dislocated by this line (on the wrong side of the ecotone) from their primary division determined by the cluster analysis. Both its location at the southern boundary of the northern hardwood forest and its rapid transition over a moderate environmental gradient are very reminiscent of the 'tension zone' in Wisconsin (Curtis, 1959). Thus we term this sharp boundary the 'New England tension zone'.

The coincidence of these changes, over roughly a town's width, ran across several physiographic sections, bedrock groups and apparently across temperature regime or altitude (Fig. 9; Table 4). For example, the tension zone included former sea coast in central Maine and the southern slopes of the White Mountains and cut diagonally across the Berkshires following neither the calcareous valley nor the Taconic ridges. Although the ecotone was generally at modest elevations (250–350 m a.s.l.) on the uplands, it did not coincide with any break in landforms or environmental variables (Grimm, 1984; Gosz, 1991). The environment of this boundary was calculated in ARCVIEW as the mean values of the seventy-nine sample towns that are within 1 km of the tension zone line (Figs 4 and 9). The tension zone obviously winds across a range of latitude (mean = 42.7°N, SD = 0.63°), but also has variable altitude (mean = 260 m, SD = 102 m), FCE-elevation (mean = −596 m; SD = 108 m), and climate (T_{bar} mean = 7.6 °C, SD = 0.7 °C). This geographically coherent boundary, despite inconsistent topography (60–350 m a.s.l.) and climate (T_{bar} range 5.7–8.6 °C), indicates a moderately low sensitivity to the regional environment. The cause of such a discontinuity in a continuous gradient may be, in part, because of a response to undetermined factors (e.g. soils, glacial substrates, bedrock), historic legacies (e.g. disturbance regimes, species migrations), or biotic interactions. Echoing the pattern in Wisconsin, a very likely cause may have been the influence of fire on the vegetation to the south of the boundary (Curtis, 1959; Grimm, 1984; Parshall & Foster, 2002).

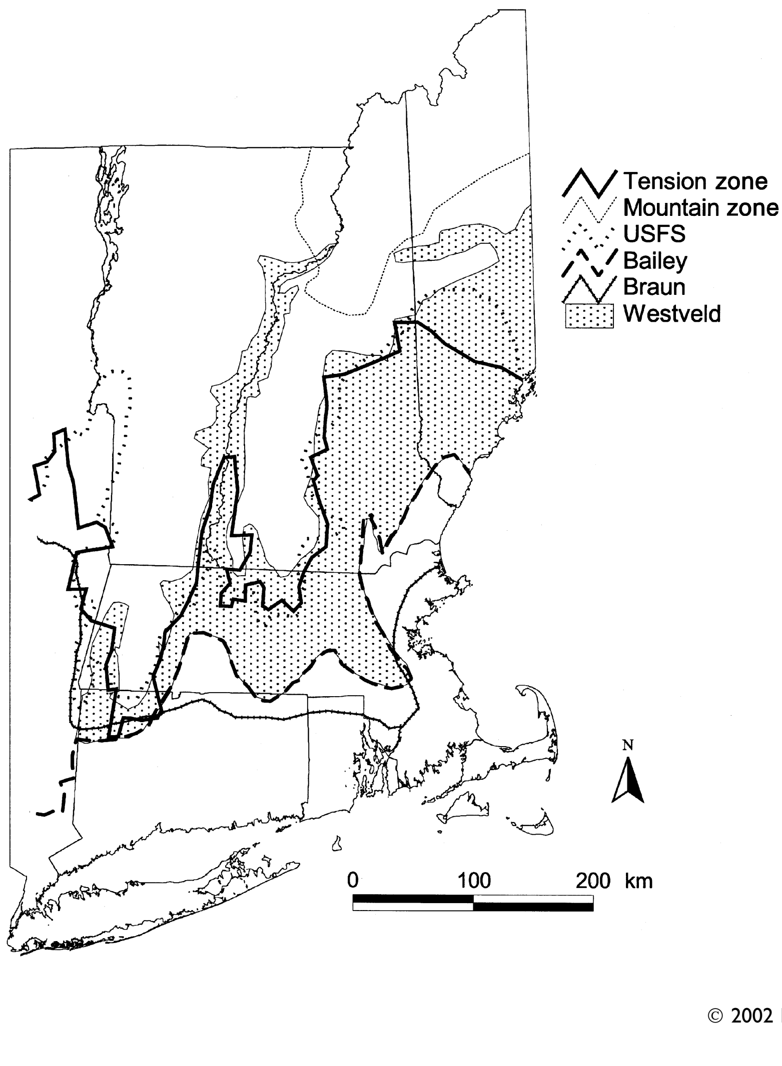

Figure 9 Location of New England Tension Zone, mapped as the town boundaries from presettlement surveys clusters. The shaded area is the extent of Westveld *et al.*'s (1956) Transition-White Pine-Hemlock Zone, which was also adopted by Kuchler (1964, 1978) as a transition zone between Northern Hardwoods and Appalachian Oak Potential Natural Vegetation and by Bailey (1976) as the boundary, in part, between the Laurentian Mixed Forest and Eastern Deciduous Forest Provinces. Also shown is Braun's (1950) boundary between the Hemlock-White Pine-Northern Hardwoods and Oak-Chestnut Regions, and the United States Forest Service's (Keys *et al.*, 1995) boundary between the Lower New England and Vermont/New Hampshire Upland Sections. The dotted line is the mountain zone boundary delimiting the extent of coniferous dominated Cluster 1.

Despite some discrepancy in the valleys, there is an obvious close correspondence between the tension zone and boundaries of previously mapped units of New England forest regions (Fig. 9). Some past studies seem to place a transition further to the south (Raup, 1940; Braun, 1950; Bailey, 1976), but the northern limits of the Westveld *et al.* (1956) transition zone aligns closely with the presettlement division. A recent compilation of ecological units in the United States (Keys *et al.*, 1995) places a modern section boundary in virtually the same location as the division in the presettlement composition, except in the southern Berkshires (Fig. 9). As these recent boundaries are all derived from modern vegetation and environmental surrogates, there is evidently a lasting and close connection between past vegetation patterns and modern, albeit altered vegetation.

Northern Hardwoods

The vegetation in the uplands of northern New England forms a single continuous sequence from mixed spruce to pure hardwoods (Fig. 5). All four northern clusters have a mixture of beech, maple and (undoubtedly yellow) birch. This is the classic 'northern hardwood' forest, with spruce gradually becoming important in the northernmost two clusters (clusters 1, 2) and hemlock increasing in the southernmost (cluster 4). Many factors of climate and topography vary in unison across the region (Table 4), such that it is difficult to separate the effects of any single factor. Significantly, the best environmental discriminator is the composite FCE-elevation index which integrates climatic factors into the complex gradient. There are also two congruent geographical gradients, altitude and latitude, but they apparently form a single vegetational sequence (Figs 6 and 7). Interestingly, the dual gradients combine to produce, on the average, clearly defined elevational 'zones' which dip to the north on the mountains (Cogbill & White, 1991). In addition, a series of distinctive hardwood species (i.e. ash, basswood, elm, butternut) were more abundant in the 'richer' environments on calcareous bedrock, in 'bottomlands' along major rivers, or in the Champlain Valley. These lowlands together with the southern edges of the region, such as north-central Massachusetts (cluster 4) also had an additional minor occurrence of southern elements (i.e. pine, oak).

The major traditional vegetational boundary in the Appalachian Mountains is the coniferous/deciduous ecotone marking the lower elevational boundary of 50% abundance of spruce-fir dominance (Siccama, 1974; Bormann & Likens, 1979; Cogbill & White, 1991). This classic montane 'coniferous' ecotone is mostly missed in the presettlement survey as high altitude sites were seldom settled and many were never surveyed. This shortfall is part of the reason that there are few sample towns in the White Mountains and it causes some 'invisibility' of montane coniferous forests on the vegetation maps (Figs 2–4).

The fourteen mixed spruce towns (cluster 1) at the northeast limits of the region certainly encompassed part of the montane coniferous zone (Fig. 4). The cluster averaged just 98-m elevation below the coniferous ecotone, but had an average maximum altitude 346 m actually above it (Table 4). A single line following the boundary of the towns in Cluster 1 delimits what we term the 'mountain zone', with only two cluster 2 towns dislocated within the zone (Figs 4 and 9). This vegetation boundary was the third division in the cluster analysis (Fig. 4), but based on the overlap of towns in the ordination (Fig. 5) and the similar composition (Table 3), it was apparently not a discontinuity on the continuum. The mountain zone lay within the Spruce-Fir-Northern Hardwood or alternatively the Northern Hardwoods Spruce zones in previous classifications (Westveld *et al.*, 1956; Kuchler, 1964), but it was more restricted, not extending down the Green Mountains or into south-western New Hampshire as in previous maps.

Within-town averaging over variable upland topography tended to dilute the proportion of any high altitude coniferous vegetation in Cluster 2, with only a shadow of the mountain zone. This originally mixed northern hardwoods cluster was warmer ($T_{\mathrm{bar}} = 6.3$ °C) and had much lower altitude (FCE-elevation $= -362$ m) than the coniferous ecotone. Despite the decrease in spruce, the 20% isowit of spruce abundance still approximated the southern boundary of cluster 2 (Fig. 3e). This boundary was also aligned with the southern boundary of the Spruce-Fir-Northern Hardwood forest zone (Westveld *et al.*, 1956). Geographically, cluster 2 filled in the areas of the modern Spruce-Hardwood Zone not occupied by cluster 1, but this combination was a low order division in the clustering (Fig. 4). Thus there are qualitatively recognizable zones in the uplands, but the priority of the relationships and the distinctiveness of any boundaries are fuzzy.

Central Hardwoods

In southern New England the topography and climate were more equitable and the prominent latitudinal/climatic gradient of the north faded. Oaks became pervasive, but did not separate into discrete contiguous geographical units. Although some clusters had geographical centres (e.g. cluster 8 in eastern Connecticut and cluster 6 on Cape Cod), they also included multiple widely scattered towns mixed among other clusters. Earlier maps delimited a distinct northern boundary of oak or 'sprout hardwoods' (i.e. chestnut, hickory, oak) at varying locations across Connecticut (Hawley & Hawes, 1912; Bromley, 1935; Braun, 1950; Westveld *et al.*, 1956). These latitudinal zones were inconsistent with the grouping of clusters that, if anything, had only a weak east–west division in Connecticut. The prevalence of oak mixed with some hickories and chestnut was obviously related to the drier conditions and perhaps disturbance (Curtis, 1959; Grimm, 1984). Precipitation was actually higher, but the temperature regime was markedly warmer than in northern New England (Table 4). More importantly, the moisture needing ('mesic') species, particularly beech (Fig. 3a), were rare except near the water (lakes, rivers or the coast). The less discrete vegetation pattern on a regional scale and the lack of a climatic gradient imply that another factor, perhaps operating at a smaller scale, is influencing the vegetation. The prominence of oaks and other 'sprout' species, the drier soils and higher temperatures, and perhaps the proximity to large indigenous populations, indicate that fire might have been the disturbance factor which was causing the non-zonal, patchy, oak vegetation (Abrams, 1992; Foster *et al*., 2002).

Central Pine

The most distinctive species pattern in central New England was the prominence of pine at the northern edge of oak dominance (Hawley & Hawes, 1912; Bromley, 1935; Jorgensen, 1971). This formed the pine-oak cluster 6 on Cape Cod and scattered towns, especially in the Merrimack Valley [also recognized by Westveld *et al*. (1956) as a unit on Cape Cod]. The more variable mixed oak transition cluster 5 was scattered from the Hudson Valley to coastal Maine. The centre of this transition was on the edge of the Seaboard Lowland where there were widespread sandy outwash soils, perhaps linking these clusters to substrate conditions. The vegetation also included scattered pine (predominantly pitch) plains (cluster 6), which presumably had a high fire regime (Parshall & Foster, 2002). This area, particularly central Massachusetts, had a considerable presettlement mixed pine component and was later the centre of the old-field white pine region (Bromley, 1935; Westveld *et al*., 1956; Foster *et al*., 1998). Interestingly, the southern edge of this oak-pine region had been proposed earlier as a prominent vegetation boundary across New England (Raup, 1940; Braun, 1950; Bailey, 1976). The presettlement surveys clearly showed (Fig. 9) the strongest vegetation boundary was near the northern edge of Westveld *et al*.'s (1956) transition zone, and that this 'transition' was vegetationally closer to oak types than to northern hardwoods.

Temperature regimes

As vegetation is a product of the climate of previous centuries, its association with current climate is indirect and dependent on a temporal equilibrium of climate patterns. Furthermore, as all presettlement surveys were carried out at the end of the 'Little Ice Age' (1450–1850), they are further removed from a modern environmental baseline. Significantly, historic climatic records from New England document a predominantly cool and somewhat wet regime from 1640 to 1820, with only short-term variability (Jones & Bradley, 1992). The coolest decade was the 1810s and the relatively stable conditions of the previous three centuries ended with a dramatic warming starting roughly in 1850 (Baron, 1992). Preliminary comparisons of early nineteenth century temperature regimes with modern averages quantify this significant increase in mean annual temperature: New Haven, CT (+1.2 °C since 1780 s); Portland, ME (+1.2 °C since 1820s); Hanover, NH (+1.7 °C since 1830s); and Amherst, MA (+1.4 °C since 1840s) (Bradley *et al*., 1987; Hamburg & Cogbill, 1988; Baron, 1992). Despite a possible slight decrease in the strength of the sea-to-upland gradient, the historic temperature changes were relatively consistent across the study area. Thus although the average climate regime has varied temporally, the spatial patterns across the region appear to be reasonably robust.

The modern climate record, at least spatially, still represents the environment which framed the geographical distributions in the presettlement surveys. The quantitative values underlying these patterns, however, must be corrected for the temporal change in the climate. The modern temperature regime can be recalibrated by −1.4 °C (average of four sites cited above) to yield an estimate of the mean annual temperature 200 years ago. For example, normalization of the current average temperature of the tension zone (7.6 °C T_{bar}), yielded an approximation of 6.2 °C for this primary boundary in the presettlement regime. Similarly, the mean annual temperature of coniferous cluster 1 (4.3 °C T_{bar}; Table 4) normalized to the eighteenth century yielded a value of 2.9 °C, which is colder (found at higher altitude) than the 3.4 °C found at the modern coniferous ecotone (Cogbill & White, 1991). If the average temperature of the boundary of the mountain zone (5.1 °C T_{bar}; Table 4, Fig. 8) is corrected by the 1.7 °C change at Hanover, it yields the same estimate of 3.4 °C for the historic coniferous boundary. Thus it appears that the contemporary temperature at the historic vegetation boundary is still appropriate today. Remarkably the presettlement vegetation distributions imply that the historic coniferous/deciduous ecotone was in a lower altitudinal position [historic crossover at 150 m below the current FCE-elevation (Fig. 6)]. This is additional evidence for the long-term decline of red spruce in the mixed forests just below the ecotone (Hamburg & Cogbill, 1988). It also indicates that significant climate change has already occurred and presettlement data are a useful quantitative baseline to document these environmental changes in the region.

Very interestingly the vegetationally discrete tension zone is typified less by temperature regime than is the mountain zone. Despite a change in climate, modern vegetation boundaries, such as the old-field pine transition zone, remains tightly bound to the historic position of the tension zone. Thus the two ecotones in New England are fundamentally different; the mountain zone is a division of a continuum which easily responds to climate, while the tension zone is sharp and responds to enduring non-climatic parameters. Apparently the mountain zone is determined by the varying abundance of a single species (spruce) that is more fluid through time than a complex vegetational tension zone involving multiple species and dynamic processes, perhaps involving fire.

Historical baseline

The witness tree sample gives both spatial and temporal perspective to the vegetation of New England that is difficult to get from previous ecological or geographical studies. Historical methods can also elucidate traditional questions. The 1700s are the appropriate baseline for judging the changes in the forest, be it the effects of logging (Williams, 1989), the role of fire (Day, 1953; Cronon, 1983), or the shifting species compositions, such as spruce or chestnut

(Hamburg & Cogbill, 1988; Paillet 2002). Significantly many prominent regional preconceptions are inconsistent with the historic data that show white pine as a minor component of the forest; spruce as prominent in the northern hardwood zone; chestnut as very restricted (< 10% of the forest); and fire as an important disturbance process throughout southern New England. Further expanded is an enigma first noted by Siccama (1963): an amazingly high presettlement proportion of beech in Vermont, a location which now supports much more maple. The presettlement data base clearly indicates this tremendous dominance of beech over all northern New England. In addition, the data base quantitatively documents many intriguing patterns of both abundance and range not seen in the previous broad-scale isowit maps (Whitney, 1994). For example, local details emerge, such as the abundance of spruce in the swamps of south-eastern New England, more than its current distribution suggests (Bromley, 1935), or the large patch of hemlock in the eastern Berkshire Hills of Massachusetts. This sample of towns is dense enough to display fine details and the extent is wide enough to show the patterns at many scales.

CONCLUSIONS

Town-wide resolution of samples and their expansive coverage were critical in documenting intermediate-scale geographical patterns in the region. The towns covered a wide range of sizes; however, all were large enough to encompass a variety of forest types and landforms, but not so large as to span major differences in physiography or climate. The town-wide scale was ideal to represent species composition of the landscape and this also matched a scale appropriate for distinguishing processes such as responses to glacial substrates or climate (Delcourt & Delcourt, 1988). Thus regional factors, such as species abundances across forest types or response to geomorphology, were detected to various degrees. For example, oak and pine vegetation, together with hickory and chestnut taxa extended northward in the large river valleys in New England. Valley influences on the presettlement vegetation, however, were more prominent in mid-river sections as the zones narrowed and the boundaries or range limits became unclear further upriver. For all the advantages of a scale which generalizes by averaging local variable composition, this method is also limited by its scale. Thus some of the valley attenuation could be the result of past species migration patterns or geomorphology in the valley itself, but much is because of the shrinking of the vegetation scale to a point at which the town-wide sample cannot detect restricted or rare elements. The town-wide surveys are ideal for describing vegetation patterns at the regional scale, but they are only an adjunct to other ecological studies of flora, palaeoecology or phytosociology.

An historical–geographical analysis of presettlement witness tree surveys gives an unparalleled picture of New England's forests before European settlement. The unbiased sampling, comprehensive spatial coverage and temporal control produce a sample that is arguably more accurate and detailed than any current description of the vegetation today (e.g. Iverson *et al.*, 1999). Analyses of the extensive data base produce maps showing spatial patterns in the vegetation as several scales. Beyond serving as direct quantitative observations of the forest unconfounded by land use history, the town-wide presettlement surveys yield a new perspective on the New England vegetation. The dominant species, oaks, beech, and to a degree spruce, determine differences in the vegetation types. Significantly hemlock, white pine and hickory seemingly are not discriminators between associations currently bearing their names (Hawley & Hawes, 1912; Braun, 1950; Westveld *et al.*, 1956). The eight clusters of towns distinguished by vegetation form a clear climatic/latitudinal series, with broad overlap of species abundances. With the exception of the dramatic oak/beech tension zone across the centre of New England uplands, the changes are gradual, the hallmark of a vegetation continuum.

Reconstructing the nature of the original forests is not just an academic exercise in historical ecology, phytogeography or vegetation ecology, but should be applied to future educational, management and conservation activities. Most importantly this historical–geographical approach establishes an empirical baseline of past species and vegetation distributions that can be used to judge both present and future changes induced by human land use or environmental change.

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Appendix 1 Names, occurrence, and equivalent synonymy of trees cited in 389 New England presettlement surveys; [ ] indicates possible secondary synonymy; A ? indicates degree of uncertainty in some identifications

Surveyor name	Towns	Stems	Taxa[†] inferred	Genus group this study
Apple	34	40	*Pyrus malus*	Other
Ash*	254	1647	*Fraxinus* sp.	Ash
Ash, Black	149	874	*Fraxinus nigra*	Ash
Ash, Mountain	1	2	*Sorbus americana, [S. decora]*	Other
Ash, Red	77	333	*Fraxinus* sp.?	Ash
Ash, Water	6	15	*Fraxinus nigra*	Ash
Ash, White	205	1118	*Fraxinus americana*	Ash
Aspen	9	37	*Populus tremuloides & P. grandidentata*	Poplars
Basswood*	182	1085	*Tilia americana*	Basswood
Beech*	293	18,731	*Fagus grandifolia*	Beech
Birch*	330	4312	*Betula* sp.	Birch
Birch, Black	171	1040	*Betula lenta*	Birch
Birch, Red	7	35	*Betula cordifolia, [B. alleghaniensis]*	Birch
Birch, Rock	19	78	*Betula* sp.	Birch
Birch, Swamp	4	60	*Betula alleghaniensis?*	Birch
Birch, White	130	577	*Betula papyrifera, B. cordifolia*	Birch
Birch, Yellow	54	315	*Betula alleghaniensis*	Birch
Blue Beech	3	7	*Carpinus caroliniana*	Ironwoods
Boxwood	20	60	*Acer negundo?*	Other
Butternut*	87	272	*Juglans cinerea*	Butternut
Buttonwood*	44	88	*Platanus occidentalis*	Buttonwood
Cedar (Atlantic)*	52	277	*Chamaecyparis thyoides*	Cedar (Atlantic)
Cedar (northern)*	52	230	*Thuja occidentalis*	Cedar (northern)
Cedar, Red	6	7	*Juniperus virginiana*	Other
Cherry*	84	154	*Prunus* sp.	Cherries
Cherry, Black	14	16	*Prunus serotina*	Cherries
Cherry, Red	5	10	*Prunus pensylvanica*	Cherries
Chestnut*	174	6841	*Castanea dentata*	Chestnut
Elm*	228	1281	*Ulmus* sp.	Elms
Elm, Red	7	10	*Ulmus rubra*	Elms
Elm, White	3	6	*Ulmus americana*	Elms
Elm, Witch	10	22	*Ulmus rubra, U. americana*	Elms
Fir*	90	669	*Abies balsamea*	Fir
Hackmetack	35	199	*Picea rubens & [Larix larcina]*	Spruces
Hard beam	16	39	*Ostrya virginiana, [Carpinus caroliniana]*	Ironwoods
Hardhack	30	171	*Ostrya virginiana, [Carpinus caroliniana]*	Ironwoods
Hazel (Witch)	62	354	*Ostrya virginiana?*	Ironwoods
Hemlock*	290	10,281	*Tsuga canadensis*	Hemlock
Hickory	11	50	*Carya* sp.	Hickories
Hornbeam	81	257	*Ostrya virginiana, Carpinus caroliniana*	Ironwoods
Hornpine	6	78	*Pinus* sp.?	Pines
Ironwood*	64	384	*Ostrya virginiana*	Ironwoods
Juniper	8	13	*Juniperus* sp.	Other
Leverwood	27	75	*Ostrya virginiana*	Ironwoods
Linden	1	1	*Tilia americana*	Basswood
Linewood	2	3	*Tilia americana?*	Basswood
Maple*	360	9900	*Acer* sp.	Maples
Maple, Hard	62	975	*Acer saccharum*	Maples
Maple, Red	1	1	*Acer rubrum*	Maples
Maple, Rock	57	309	*Acer saccahrum*	Maples
Maple, Soft	58	466	*Acer rubrum, [A. saccharinum]*	Maples
Maple, Sugar	5	10	*Acer saccahrum*	Maples
Maple, Swamp	2	3	*Acer rubrum, [A. saccharinum]*	Maples
Maple, White	50	190	*Acer saccharinum, [A. rubrum]*	Maples
Mulberry	1	2	*Morus rubra*	Other
Oak	235	1961	*Quercus* sp.	Oaks
Oak, Black	264	16,733	*Quercus rubra* & *Q. velutina*	Oaks

Appendix 1 *continued*

Surveyor name	Towns	Stems	Taxa[†] inferred	Genus group this study
Oak, Chestnut	41	174	*Quercus prinus*	Oaks
Oak, Grey	59	799	*Quercus rubra*?	Oaks
Oak, Mountain	3	7	*Quercus prinus*?	Oaks
Oak, Pin	18	28	*Quercus palustris*	Oaks
Oak, Red	237	7548	*Quercus rubra*	Oaks
Oak, Rock	37	551	*Quercus prinus*?	Oaks
Oak, Shrub	9	15	*Quercus ilicifolia*?	Oaks
Oak, Swamp	46	256	*Quercus bicolor*	Oaks
Oak, White*	271	32,635	*Quercus alba*	Oaks
Oak, White Swamp	18	54	*Quercus bicolor*	Oaks
Oak, Yellow	32	145	*Quercus prinus*	Oaks
Oilnut	5	16	*Juglans cinerea*	Butternut
Peach	2	2	*Prunus* sp.?	Cherries
Pear, Wild	11	23	*Prunus* sp., [*Amelanchier* sp.]	Cherries
Pepperidge*	34	114	*Nyssa sylvatica*	Pepperidge
Pine*	259	9629	*Pinus* sp.	Pines
Pine, Black	3	4	*Pinus* sp.?	Pines
Pine, Candle	4	39	*Pinus* sp.?	Pines
Pine, Norway	16	44	*Pinus resinosa*	Pines
Pine, Pitch	119	2642	*Pinus rigida*	Pines
Pine, Red	2	2	*Pinus resinosa*	Pines
Pine, Spruce	7	13	*Tsuga canadensis*?	Pines
Pine, Swamp	3	3	*Pinus* sp.?	Pines
Pine, White	189	2403	*Pinus strobus*	Pines
Pine, Yellow	15	29	*Pinus rigida*, [*P. resinosa*]	Pines
Plum	9	16	*Prunus* sp., [*Amelanchier* sp.]	Cherries
Poplar*	194	1188	*Populus* sp.	Poplars
Poplar, Water	3	22	*Populus* sp.?	Poplars
Popple	25	86	*Populus tremuloides* & *P. grandidentata*	Poplars
Remmond	4	15	*Ostrya virginiana*?	Ironwoods
Roundwood	4	7	*Sorbus* sp., [*Acer pensylvanicum*]	Other
Shagbark	4	7	*Carya ovata*	Hickories
Spruce*	229	4533	*Picea rubens* [*P. mariana, P. glauca*]	Spruces
Spruce, Black	12	77	*Picea rubens* & [*P. mariana*]	Spruces
Tamarack*	21	58	*Larix laricina*	Tamarack
Walnut*	230	7927	*Carya* sp.?	Hickories
Walnut, Bitter	3	4	*Carya cordiformis*	Hickories
Walnut, Black	2	2	*Juglans nigra*	Other
White Tree	5	6	*Liriodendron tuliperfera*?, [*Tilia americana*] & [*Populus deltoides*?]	Other
Whitewood	46	187	*Liriodendron tuliperfera*?, [*Tilia americana*] & [*Populus deltoides*?]	Other
Wicerpee	10	32	*Tilia americana*?	Basswood
Odd Oaks (*Quercus* sp.): (Name Towns, Trees)	Greene 2, 54; Blue 2, 9; Clapboard 2, 3; Shingle 1, 2; Beach 1, 1; Chasson 1, 1; Live 1, 1; Pinknot 1, 1; Red Rock 1, 1; Ruff 1, 1; Squirrel 1, 1; Swamp Black 1, 1			
Ambiguous species: (Name Towns, Trees)	Swampwood 12, 50; Pegwood 5, 15; Hornwood 4, 8; Beattlewood 3, 18; Bilberry tree 4, 6; Black tree 3, 5; Clapboard 3, 3; Shittum wood 2, 2; Ballwood 2, 2; Jerwood 2, 2; Navewood 2, 2; Feare? 1, 8; Caven 1, 3; Tobaccowood 1, 2; Dogberry 1, 2; Chebalo tree 1, 2; Almond tree 1, 1; Bigwood 1, 1; Greenwood 1, 1; Mastick 1, 1; Nickopwood 1, 1; Pipestaff 1, 1, White Ash Poplar 1, 1; Rauge 1, 1			

*Lead taxa in one of the twenty-two lumped genus categories.
[†]Nomenclature follows Gleason & Cronquist (1991).